Coral reef status and trends of North Ari islands under different management regimes (2015-2019)

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This publication has been made possible in part by generous funding from USAID.

This research has been made possible with the collaboration and expertise of Ministry of Environment, Environmental Protection Agency (EPA), and Maldives Marine Research Institute (MMRI).

The authors would like to acknowledge the following individuals for their assistance and support in the design and development of the project and collection of data over the survey period: Ameer Abdulla, Fathimath Hana Amir, Dominic Bryant, Fredric Caldwell, Zachary Caldwell, Benjamin Cowburn, Akram Elkateb, Michael Fox, Kathryn Furby, Gabriel Grimsditch, Maleeha Ibrahim, Nizam Ibrahim, Ashwag Ismail, Abdulqader Khamis, Paul Marshall, Maeesha Mohamed, Paul Retson Muir, Azim Musthag, Fathmath Nistharan, Chiara Pisapia, Mahid Abdul Rahman, Saaif Mohamed Rasheed, Amir Schmidt, Silvia Spezzaferri, Michael Sweet, Hussein Zahir and Brian Zgliczynski

The crews of the M/V Theia, the M/V Leo of Constellation fleet and M/V Soleil 2 who provided vessels and equipment, ensuring we could collect all the necessary data.

We are grateful to Najfa Shaheem Razee and Fathmath Shihany Habeeb for reviewing the report and providing detailed feedback.

Published by: IUCN and the Government of Maldives in collaboration with USAID

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Citation: Dryden, C., Basheer, A. Moritz C., Birrell, C. (2020). *Coral reef status and trends of North Ari islands under different management regimes (2015-2019)*

Malé, Maldives: IUCN and Government of Maldives. xx pp.

Cover photo: © Ahmed Basheer, IUCN Maldives

Produced by: IUCN Maldives, Malé, Maldives

Executive summary

Coral reefs are currently subject to an array of pressures acting across global and local scales. Many of these are linked to unprecedented rates of change in global temperatures and atmospheric concentrations of CO_2. Climate change is now widely considered as the greatest threat to the continued existence of coral reefs. One consequence of increase global temperatures is an increased frequency and severity of coral bleaching events. Since the turn of the century there have been four bleaching events that have impacted reefs worldwide. Local stressors such as overfishing, declining water quality and coastal development compound these global level threats. Reefs under greater local stress generally are less resistant to acute warming events and are likely to experience more severe bleaching.

Coral reefs are dynamic and interconnected systems in which impacts causing changes in the health and cover of corals have wide impacts on overall ecosystem health and functioning. Corals create the complex three-dimensional structure that the reef community inhabits. There are several factors that may increase the resilience of the reef ecosystem to the impacts of bleaching events, and managers face the challenge of mitigating global stressors by enhancing local resilience.

The Maldives archipelago is a chain of coral reefs and islands lying the tropical central Indian Ocean with 4,513 km^2 area of shallow reef, 26 atolls, and 1192 low lying islands. Island use can be grouped into three categories of community islands, resort islands and uninhabited islands. Each island category represents a different island use, with different rules and impacts on the island's reef area and this distinction can be used as a proxy for marine management regime. Coral reefs in the Maldives were severely impacted by the 2016 global bleaching event, with approximately 73% of corals on shallow (<13 m) reefs bleaching. Reefs are also threatened by a range of local scale factors including dredging, island building and pollution.

The reefs surrounding 12 islands in North Ari Atoll were surveyed one year before the bleaching event: 22nd to 4th of May 2015, during the bleaching event: 15th to 30th May 2016

and three years after the bleaching event: 26^{th} June to 7^{th} of July 2019. Underwater visual census was used to collect data on coral reef substrate, coral and fish communities and reef structure. This data was used to examine the impact of the bleaching event on the coral reef habitat and the relationships with management and habitat conditions.

The 2016 mass bleaching event resulted in a significant decline in coral cover, coral diversity, lower coral recruitment, reduced fish biomass and declines in the key fish groups at North Ari Atoll. Reefs have undergone a severe decline in structural complexity resulting in flattening of reef habitat and a reduction in the three-dimensional reef matrix which is vital in supporting diverse reef assemblages. The structural degradation has been accompanied by an increase in the proportion of reef substrate comprised of sand and a subsequent decline in suitable solid habitat for settlement or growth of corals. The reef fish community has suffered corresponding declines in density, diversity and biomass. These impacts were noticeable across all fish groups and families examined. Management regime appears to have had little effect in limiting the negative consequences of the bleaching event.

Coral cover declined from an average of around 20% across all sites in 2015 and 2016 to an average of 8 % in 2019. The impact of the bleaching masked any potential management effect in this study, though the analysis did find a number of significant interactions between management and habitat conditions. This may indicate that the effects of management vary depending on the environment. Turf algae remained consistently high (approximately 25 – 30 % of substrate cover) across years, management and environmental gradients. Crustose coralline algae cover fluctuated over the three survey years, apparently having been impacted by the bleaching in 2016 before returning to pre-bleaching levels in 2019. Macroalgae cover was generally low across all years, management and environmental gradients.

Since 2016 there has been an approximate 30 % increase in the proportion of the reef substrate that is occupied by sand at North Ari Atoll. An increase in sand of this magnitude is consistent with the degradation of a reef community, widespread mortality of corals and progressive erosion of the structure built by corals and other calcareous organisms structure. The most serious implication of a greater proportional cover of the substrate by sand is the reduction in suitable habitat for benthic organisms.

In 2016, all coral genera were impacted to variable extents by bleaching. At the time of the 2016 survey, which was undertaken mid bleaching event, dead colonies were observed for 26 genera. Of the four most commonly observed coral genera *Acropora* were found to be the genus most sensitive to coral bleaching, undergoing a significant decline in percent cover. The other three, *Porites, Pocillopora and Pavona*, either had no or small changes in cover following the bleaching event.

The bleaching event appears to have had severe impacts across the entire fish community, with total biomass and fish density dropping approximately 70 % and 50 %, respectively, between 2015 (before bleaching) and 2019. Management regime appears to have had little if any effect on the overall condition of the fish community, suggesting the impact of bleaching may have been stronger than any recent human pressures. The biomass dropped so dramatically everywhere that it is difficult, at present, to determine any differences across the surveyed islands that could be attributable to anthropogenic pressures.

The decline in herbivore biomass between 2015 and 2016 appears to have been driven by a significant drop in the biomass of parrotfish that occurred across all management regimes. The overall decline in herbivore biomass, particularly large roving herbivores such as parrotfish, is concerning given the important functional role this group has on reef functioning. Herbivores play a key functional role on reefs by feeding on the algae, preventing them from outcompeting corals, thus favouring coral recruit settling and growth necessary to reef resilience.

The status of the reef fish community in 2019 shows the important role that physical conditions for the reef communities of North Ari and their response to the 2016 bleaching event. Though community islands have significantly higher biomass and diversity than resort or uninhabited islands, this difference is driven by high numbers at outer atoll reefs. Inner atoll islands consistently had lower values for all three fish community metrics, regardless of management regime. When islands were grouped by inner or outer atoll location, outer atoll islands had significantly higher values for fish community density, diversity and biomass.

The habitat structure of reefs in North Ari Atoll became less complex after 2016. The complexity of a reef habitat is largely associated with three-dimensional structure that is created by live corals The reduced complexity of reefs at North Ari Atoll, regardless of management regimes, is consistent with observations of degraded reefs losing live coral and the structure created by live corals.

Management benefit from resorts has been identified previously, yet our findings indicate that any benefit may have been blurred by the impacts of the bleaching event. The reefs on outer atoll islands with access to ocean currents and experience greater water exchange, were in better condition in 2019 than inner atoll reefs which have calmer waters where temperature rises substantially every day, leading to intensified heat stress for corals. Regardless of the management regime in place on an island, it is important that coral reef management efforts are employed to help protect the reefs and each management type will have its own challenges.

Two key management recommendations are:

1) Sensitive habitats such as sheltered reefs and inner atoll islands have been shown to be more susceptible to the effects of human impacts. Therefore, these areas should be more closely monitored, with tighter restrictions on activities

2) Marine protected areas should be created at the more resilient habitats, such as outer atoll or exposed reef locations. These are more likely to withstand natural disturbances that cannot be managed locally, such as bleaching.

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1. Introduction

Coral reefs are currently subject to an array of pressures acting across global and local scales. Many of these are linked to unprecedented rates of change in global temperatures and atmospheric concentrations of CO_2 (IPCC 2014). Climate change is now widely considered as the greatest threat to the continued existence of coral reefs (Hughes et al. 2003b, 2007). Rising ocean temperatures lead to an increase in extreme weather events (Herring et al. 2018), coral disease outbreaks (Bruno et al. 2007) and potentially, most devastatingly, coral bleaching events (van Oppen and Lough 2018). Coral bleaching is a stress response in corals where they lose some or all of their symbiotic algae (*Symbiodinium* spp.). Bleaching is not a new occurrence and has likely happened historically on small spatial scales in response to localised stresses.

Widespread bleaching events can occur when large areas of coral reefs are exposed to temperatures beyond their thermal threshold. The most severe of these caused over 80 per cent of corals to bleach in the Caribbean and a decline in average coral cover from 42% to 2% in the Maldives (Eakin et al. 2010). Additional effects of high temperatures include stress to the coral, which can leave them more susceptible to disease or competition for space and resources on reefs (Hoegh-Guldberg 1999, Hughes et al. 2003a). Without efforts to mitigate climate change, 99% of the world's Marine Protected Areas (MPAs) are forecasted to warm ≥2 °C by 2100 (IPCC 2014). Even a mitigation scenario that limits warming rates to roughly 50% lower than no mitigation would result in mean warming rates of 0.014 °C per year in tropical MPAs (IPCC 2014). It is suggested that the threat of mass bleaching events will continue to increase over the next century (Bruno et al. 2018).

Local stressors to coral reefs compound these global level threats. These include overfishing, declining water quality and coastal development (Hughes et al. 2007, Carilli et al. 2009, Burke et al. 2011, D'Angelo and Wiedenmann 2014). These stressors tend be more chronic in nature, causing a slow degradation of the reef over time. Reefs under greater local stress generally are less resistant to disturbances such as acute warming events and are likely to experience more severe bleaching (Carilli et al. 2009). Localised disturbances resulting from construction projects or land reclamation, can also result in the physical destruction of areas of reef, particularly where adequate impact assessments are not conducted.

Coral reefs are dynamic and interconnected systems in which impacts that lead to changes in the health and cover of corals have wide impacts on overall ecosystem health and functioning. Many reef fish are reliant on corals for food (Cole et al. 2008), habitat (Pratchett et al. 2018) and/or settlement (Coker et al. 2012). Corals create the complex three-dimensional structure that the reef community inhabits. The initial loss of coral cover may have few direct effects on species of fish and invertebrates except for those that feed directly on the coral. However, over time the degradation and erosion of the reef structure can have widespread impacts on these entire communities.

The composition of the substrate may also undergo significant changes. Immediately following severe disturbance events that cause high coral mortality there is an increase in area available for new growth and settlement. Re-settlement of this area by new coral recruits depends on three key factors: a sufficient supply of coral larvae (Hughes and Tanner 2000), competition for space (Kuffner et al. 2006, Johns et al. 2018) and predation (Cole et al. 2008, Doropoulos et al. 2013). Areas of unconsolidated substrate such as sand or rubble from eroded coral skeletons hinder coral recruitment (Chong-Seng et al. 2014). Consolidated surfaces such as substrates bound by crustose coralline algae (CCA) can be more favourable for recruitment (Yadav et al. 2016). The survival rate of coral recruits increases with size and most corals survive once they are 5 cm in diameter (Doropoulos et al. 2015). These provide an indication of the corals likely to grow to a reproductive size and contribute to reef recovery.

There are several factors that may increase the resilience of the reef ecosystem to the impacts of bleaching events, and managers face the challenge of mitigating global stressors by enhancing local resilience. The trajectory of coral reefs following bleaching events can differ under different management regimes (Mellin et al. 2016). Protection of herbivorous fish that graze on algae can contribute to reef recovery (Mumby et al. 2006). Herbivores are important for maintaining coral reef resilience and preventing transitions to non-coral dominated state by grazing on algae which can inhibit coral settlement and growth (Graham et al. 2013, Hixon 2015). Structural complexity is positively associated with reef fish diversity and the degradation of reef structure may result in reduced abundance and diversity (Graham et al. 2007, 2015, Newman et al. 2015), which can impact reef resilience. Structural complexity is also one of several biophysical processes that can enhance coral recruitment following disturbances (Gouezo et al. 2020). Therefore, maintaining reef complexity can substantially increase reef resilience in the long term.

For the purpose of this study, island use has been grouped into three categories of community islands, resort islands and uninhabited islands. This distinction is a proxy for marine management regime (Moritz et al. 2017). Uninhabited islands have no permanent human population and the land is either relatively untouched by people or used for agricultural or industrial activities. These islands have no true fishing regulation and therefore can experience heavy fishing pressure without management (Majeedha 2017). Resort islands are dedicated to tourism and are de-facto no-take zones with fishing other than light recreational fishing forbidden (Majeedha 2017). Influences of resort islands on reefs include regular sand dredging for beaches, coastal construction, sewage and waste, and impacts associated with recreational activities (e.g. coral trampling) (Zahir 2002). Reefs surrounding community islands are generally expected to experience a higher degree of human influence, which may include coastal construction, sewage and waste, and fishing by local populations (Zahir 2002, Majeedha 2017).

In 2015, 2016 and 2019, ecological surveys were undertaken in North Ari Atoll under REGENERATE, a Government of Maldives Project, implemented by IUCN and generously funded by USAID, to assess ecosystem health in islands under different management regimes. This report presents data collected during the most recent surveys, undertaken in July 2019, and compares these with data collected in 2015 and 2016. Maldives experienced a severe bleaching event in April-May 2016, which impacted many reefs (Ibrahim et al. 2017). This report explores two questions: 1) how have the state of reefs in North Ari changed following the 2015/2016 bleaching event between 2015 (before the bleaching event), 2016 (during the bleaching event) and 2019 (after the bleaching event) and 2) does the management regime have any correlation to the trajectory of reefs following the bleaching event.

2. Methods

2.1. Study Site

The Maldives extends between 7° 06’ 35” N to 0° 42’ 24” S and 72° 33’ 19” to 73° 46’ 13” E in the central Indian Ocean (Risk and Sluka 2000). This includes a 4,513 km^2 area of shallow reef, 26 atolls, and 1192 low lying islands, the largest island is 6 km^2 in land area. Ari Atoll is 90 km long and 32 km wide and located in the western centre of the Maldives (Figure 1). North Ari Atoll is an administrative unit comprising the northern half of Ari Atoll, Thoddoo island and Rasdhoo Atoll and extends over 960 km^2, including 80 reef systems and a shallow reef area of 170 km^2. North Ari Atoll includes 13 resorts, each located on its own island, and is a popular tourist destination due to its proximity to Malé (Majeedha 2017).

In 2016, North Ari Atoll was impacted by a coral bleaching event associated with sea surface temperatures (SST) that were above the reported threshold of 30.9° C for the Maldives during April and May (Pisapia et al. 2016, NOAA 2017, Cowburn et al. 2019). Peak temperature of 31.5° C was recorded on the 2nd of May at a 10 m depth by a temperature logger placed at Rasdhoo Island. Reports indicate 73.1% of corals bleached in the Maldives during this time period (MRC 2017, Cowburn et al. 2019), whilst bleaching was observed in 58.8% of mature coral colonies (> 5 cm diameter) in simultaneous surveys of the sites visited for this study (IUCN unpublished).

The reefs surrounding 12 islands in North Ari Atoll were surveyed (Figure 1, Table 1) one year before the bleaching event: 22nd to 4th of May 2015, during the bleaching event: 15th to 30th May 2016 and three years after the bleaching event: 26th June to 7th of July 2019.. These reefs were characterised by three management regimes that represent different levels of human presence and influence on reef systems: community islands (Bodufolhudhoo, Feridhoo, Maalhos, and Rasdhoo), exclusive tourist resorts (Kandholhudhoo, Madoogali, Maayafushi, and Velidhoo), and uninhabited islands with Maldivian villages (Gaathafushi, Madivaru, Alikoirah, and Vihamaafaru). Islands can also be classified by location within an atoll. Island located on the outer rim of an atoll are more exposed to waves and ocean currents. Islands within the atoll are more sheltered from waves and currents and will a more stable environment. Half the islands surveyed here were on the exposed out atoll rim and half were sheltered inner atoll islands, however these were not evenly distributed by management regime.

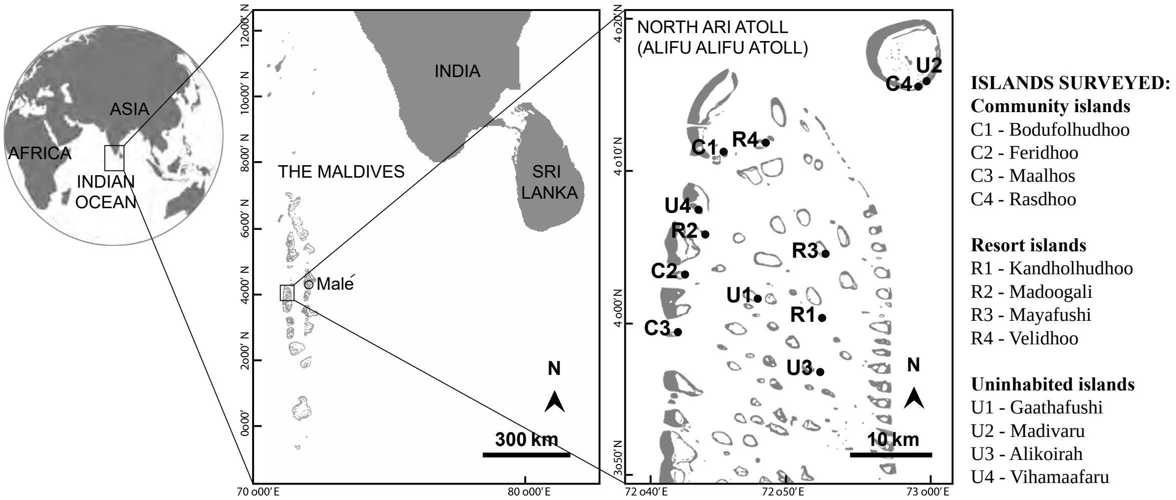


Figure 1. Location of the North Ari survey locations

Table 1. Islands surveyed around North Ari Atoll

Island Name	Date 2015	Date 2016	Date 2019	Management regime	Exposure	Latitude	Longitude	Location
Bodhufulhudhoo	23/04/2015	20/05/2016	27/06/2019	Community	Inner	4.185382	72.773371	Atoll lagoon
Feridhoo	26/04/2015	24/05/2016	30/06/2019	Community	Outer	4.051062	72.726221	West rim
Maalhos	27/04/2015	27/05/2016	01/07/2019	Community	Outer	3.98617	72.719693	West rim
Rasdhoo	22/04/2015	17/05/2016	26/06/2019	Community	Outer	4.262551	72.992096	South rim
Kan'dholhudhoo	29/04/2015	28/05/2016	05/07/2019	Resort	Inner	4.002328	72.881792	Atoll lagoon
Maayafushi	01/05/2015	29/05/2016	06/07/2019	Resort	Inner	4.073512	72.887618	Atoll lagoon
Madoogali	02/05/2015	22/05/2016	02/07/2019	Resort	Outer	4.09598	72.752951	West rim
Velidhoo	24/04/2015	19/05/2016	28/06/2019	Resort	Inner	4.194772	72.818715	Atoll lagoon
Alikoirah	30/04/2015	26/05/2016	04/07/2019	Uninhabited	Inner	3.943425	72.88064	Atoll lagoon
Gaathafushi	28/04/2015	25/05/2016	03/07/2019	Uninhabited	Inner	4.023119	72.810783	Atoll lagoon
Madivaru	04/05/2015	18/05/2016	07/07/2019	Uninhabited	Outer	4.26938	73.00092	East rim
Vihamaafaru	03/05/2015	21/05/2016	29/06/2019	Uninhabited	Outer	4.121954	72.746492	West rim

2.2. Data collection

At each reef, three sites were surveyed by scuba diving on the reef slope at 10 m depth (± 1 m according to tide and reef structure) (Figure 2). Sites were chosen to be representative of the island, i.e. have at least one or two sites on the side of the island that were exposed to the main current and one or two sites in a more sheltered area. At each site, three 50 m transects (considered as replicates) were placed parallel to the reef contour and separated by approximately 5 m (to ensure statistical independence between replicates). Along these transects, observations were made of the fish community, mature coral community, coral recruits and general benthic community by different observers diving at the same time.

Figure 2. Data collection during the 2019 North Ari surveys.

2.2.1. Substrate

Point intercept transects (PIT) were used to describe the benthic community at each site. The biota or abiotic substrates were identified at points every 50 cm along each 50 m transect, generating 100 observations per transect (Facon et al. 2016). The benthic biota or abiotic substrate at each point was described to the level of life form categories. Greater detail was recorded for corals, soft corals and macroalgae, which were identified to the level of genus. The state of each coral was also described differentiating corals as normal, bleached, or recently dead. Recently dead specifically identifies corals that have died recently enough for there to be no growth of algae or other fouling organisms on the dead coral, normally indicating the coral died within days to a week. Care was taken to differentiate bleached corals and corals dead as a result of bleaching from corals killed by Crown of Thorns Starfish (COTS) by looking for COTS and COTS feeding scars. Percent cover of substrate categories are reported as median values with interquartile ranges (IQR).

2.2.2. Coral community

Detailed observations of the coral genus and size class were undertaken in a 10 m × 1 m belt transect survey at the start of each 50 m transect. All corals encountered were identified to genus and allocated to size classes of 6 to 10 cm, 11 to 20 cm, 21 to 40 cm, 41 to 65 cm and larger than 66 cm, based upon their maximum diameter. The state of each coral was also recorded differentiating corals as normal, bleached, or recently dead as described for the PIT surveys. Abundance of corals are reported as median values with interquartile ranges (IQR).

2.2.3. Coral recruits

Coral recruits were defined as coral colonies less than 5 cm in maximum diameter. Recruit maximum diameter was measured in millimetres using callipers and recruits were identified to the level of genera. The state of coral recruits was distinguished between "alive and healthy", "alive and bleached", and "recently dead". Partially bleached recruits were extremely rare and therefore included in one of the previous categories. "Recently dead" status was determined on the basis of the absence of overgrowth by microorganisms and filamentous algae, in order to include only recruits that had died within two weeks prior to observations and most likely as a result of bleaching (Diaz-Pulido and McCook 2004).

Recruit abundance was surveyed along the first 5 m to 10 m of each transect within a belt of 0.5 m width. The exact length of belt transects used to survey recruit abundance varied according to the abundance of coral recruits and substrate complexity, which determined the time necessary to search for recruits. Approximately 30 minutes was allocated to searching for recruits along each transect to standardise the search effort.

To estimate the surface area and proportion of substrate available for recruitment, reef rugosity and substrate data from the Point Intercept Transects (PIT) were used. Raw recruit abundance data was calibrated to consider the proportion of substrate available to recruits by discarding unconsolidated substrate, e.g. sand, which corals do not usually recruit on. Recruit abundance was also standardised to area searched according to transect rugosity (Rylaarsdam 1983). Abundances of coral recruits are reported as median values within Interquartile Ranges (IQR).

2.2.4. Analysis of the benthic community

Analysis of the benthic community was done using all 108 transects as replicates of the North Ari surveys in 2015, 2016 and 2019. A linear mixed effects analysis was used to assess how the percent cover of the substrate categories collected on point intercept transects was affected by management, year, island exposure, local exposure, history of COTS and local reef gradient. We considered these all to be fixed effects, and included interaction terms for management * island exposure, and management * local exposure into the model. As random effects, we had intercepts for islands and sites, as well as by-island and by-site random slopes for the effect of management. All analysis was conducted in R (R Core Team 20202) and models were run using the lme4 package (Bates et al. 2015).

Visual inspection of residual plots was used to detect any deviations from homoscedasticity or normality. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. The most parsimonious models was selected based on likelihood ration tests and Aikaike information criterion (AIC).

2.2.5. Fish community

All species of fish were counted by four observers on the three 50 m transects at each site. Smaller, territorial or cryptic species were counted on a 2 m wide belt, and larger, more mobile species on a 5 m wide belt (Table A2). Individual fish were identified to species, their abundance was counted, and their size estimated to the nearest 1 cm, for fish less than 20 cm, and to 5 cm for larger fish. Species were assigned trophic groups based on literature and dietary information (Froese and Pauly 2017), i.e. herbivore, carnivore, corallivore and planktivore. Fish species strongly dependant on coral for food and/or for habitat were considered as "coral-related" species. The biomass of fish species was calculated using length-weight conversion: $W = aL^b$, where a and b are constants, L is total length in centimetres and W is weight in grams. Constants vary by species and were collected from experts and scientific studies or where data was otherwise unavailable from FishBase (Froese and Pauly 2017). Diversity was calculated as the number of species per transect.

Sampling units varied by fish species (small or large), therefore all results were presented per 100 m^2. The temporal trends in the fish data of 2015, 2016 and 2019 were investigated for total fish density, diversity and biomass. The fish data was analysed for different fish trophic groups: herbivore, carnivore, corallivore and planktivore, and for the habitat- associated "coral-related" group and for key fish families: parrotfish (Scaridae), surgeonfish (Acanthuridae) and rabbitfish (Siganidae), groupers (Serranidae) and wrasse (Labridae). The analysis was performed on data from 2015, 2016 and 2019, per management regime and position of the island in the atoll where relevant, as described in the statistical analysis below.

2.2.6. Analysis of the fish community

Temporal analysis was done using all 108 transects as replicates of the North Ari surveys in 2015, 2016 and 2019. A repeated measure Analysis of Variance (ANOVA) was performed to estimate the significance of time, used as an independent variable (3 levels, i.e. pre-bleaching: 2015; during bleaching: 2016; and post-bleaching: 2019) on the fish metrics. Post-hoc Tukey

Honest Significant Differences (HSD) tests using Bonferroni correction were performed after the ANOVA to estimate significant differences between years.

To assess the current (2019) status of the reef fish community in North Ari, a one-way ANOVA was used to analyse the differences among group means in the density, diversity and biomass of the fish community and the trophic, coral-related and family groups described above using only the 2019 fish data. Two factors were tested 1) island management regime (levels 'community', 'resort' and 'uninhabited') and 2) island position within North Ari atoll (levels 'inner' and 'outer'). Because interactions between factors were not significant, only simple main-effects were tested. Fish density and biomass were log-transformed prior to analysis when necessary to satisfy the assumptions of homoscedasticity and normally distributed residuals. Post hoc Tukey's HSD tests were performed to determine the source of any significant interactions between management regimes and between island positions. For all analyses, the p-value threshold considered for significance was 0.05.

2.2.7. Rugosity of the reef substrate

Reef rugosity was measured using a 10 m long, fine-linked chain at the start of the transect. The chain was carefully fitted to the substrate contour, hugging crevices and structures, along the initial section of each 50 m transect. The linear distance to the point where the chain fitted to the substrate ended was recorded from the transect tape. To calculate rugosity (R), the linear distance of the fitted chain in cm was subtracted from 100 (the length of chain in cm).

Rugosity = linear length of fitted chain (cm) – length of chain laid flat (cm)

2.2.8. Seawater temperature

Seawater temperature was recorded at depths of 10 m starting from June 2016 using HOBO Water Temperature Pro v2 Data Loggers. Individual loggers were attached to the substrate in the vicinity of the survey transects and were set to record temperature at intervals of 30 minutes. Loggers were placed in cryptic locations to avoid direct sunlight and protected within a plastic tube that allowed for water circulation. During the 2019 survey, the loggers were collected. Only 17 of the 24 deployed loggers were retrieved. Based upon the maximum monthly mean temperature (MMM) of 2018, when bleaching was not reported in the Maldives, a temperature of ~ 30.9 ˚C is initially suggested as a bleaching threshold temperature for North Ari Atoll at 10 m depth.

3. Results

3.1. Substrate cover

3.1.1. Benthic community composition in 2015, 2016 and 2019

In both 2015 and 2016, the benthic community of reefs from all three management regimes was dominated by hard corals and turf algae (Figure 3). Coral cover was similar across all surveyed reefs between 2015 (median: 23.5 % IQR 11.0 %, 32.3 %) and 2016 (median: 20.0 % IQR 11.0 %, 31.0 %) in 2016. The percent cover of hard coral declined significantly from 2016 to 2019 (df = 307.3, $p < 0.01$) across all management regimes in 2019 by an average of 11.4 % (± 1.5 S.E.), to a median of 8.0 % (IQR 2.0 %, 15.3 %). However, coral cover at community island reefs (median 14.0 % IQR 10.0 % - 19.3%) was greater than at both resort (median 2.0 % IQR 1.0 % - 8.0%) and uninhabited island reefs in 2019 (median 4.5 % IQR 2.0 % - 15.3%). The effect of management on the percent cover of corals was influenced by (differed as a result of) island exposure (χ^2(df = 2) = 6.1, $p < 0.05$).

Turf algae cover was similar for all years (χ^2(df = 2) = 1.2, $p > 0.05$) management regime (χ^2(df =2) = 3.8, $p = 0.05$). Median cover of turf algae was 25.0 % (IQR 18.0 %, 33.3 %) in 2015, 27.0 % (IQR 21.0 %, 35.0 %) in 2016 and 26.5 % (IQR 17.0 %, 38.0 %) in 2019. Crustose coralline algae (CCA) had the third highest cover of the living benthic categories. The cover of CCA varied significantly (χ^2(df =2) = 58.3, $p < 0.01$) across all three years. Declining from a median cover of 4.0 % (IQR 2.0 %, 8.0 %) in 2015 to 2.0 % (IQR 0.0 %, 3.0 %) in 2016 before increasing to 5.0 % (IQR 2.0 %, 8.0 %) in 2019. The effects of management on CCA cover differ according to island exposure (χ^2(df = 2) = 7.2, $p < 0.05$) that indicated percent cover of CCA was greater on exposed outer atoll resort island reefs than on the sheltered inner atoll community island reefs.

Cover of all other living benthic categories was below 5 % (Table 2). Macroalgae cover was similar across years and management regimes. The highest cover of macroalgae was observed in 2016 on uninhabited island reefs (median 3.0 % IQR 1.0 %, 5.5 %). In 2019 macroalgae were rarely seen and macroalgae cover had declined at most reefs. Sponges were more frequently observed in 2016. The cover of sponges increased slightly by 2019 for community and resort island reefs but was greater on uninhabited reefs. Cyanobacteria were rarely observed but were most frequently present at community island reefs. Soft corals were also rare and primarily observed at community island reefs. Other invertebrates were occasionally observed at uninhabited island reefs and at community island reefs, but infrequently at resort island reefs. The cover of other invertebrates increased for community island reefs and uninhabited island reefs in 2016. The cover of other invertebrates remained relatively similar in 2019.

Proportion of the reef surface covered by sand was similar between 2015 and 2016 but increased on average by 13.0 % (±1.7 % S.E.) in 2019, (χ^2(df =2) = 310.7, $p < 0.01$). Cover of sand did not differ significantly between management regimes or between inner and outer atoll islands (χ^2(df =1) = 0.5, $p > 0.05$).

The percent cover of rubble was similar between 2015 and 2016 but declined by a mean of 24.4 % (±1.6 %) in 2019, (χ^2(df =2) = 207.4, $p < 0.01$). The cover of rubble was higher at resort (median: 33.5 % IQR 15.5 %, 56.8 %) and uninhabited island reefs (median: 24.5 % IQR 8.8 %, 44.3%) than at community island reefs (median: 0.0 %IQR 0.0 %, 18.0 %) in 2015. The cover of rubble increased at community island reefs to reach similar levels to resort and uninhabited island reefs in 2016. Rubble cover declined at all management regimes and covered a median value of less than 15 % of the of the habitat in 2019. The percent cove of rubble did not differ between inner and outer atoll reefs (χ^2(df =1) =1.0, $p > 0.05$).

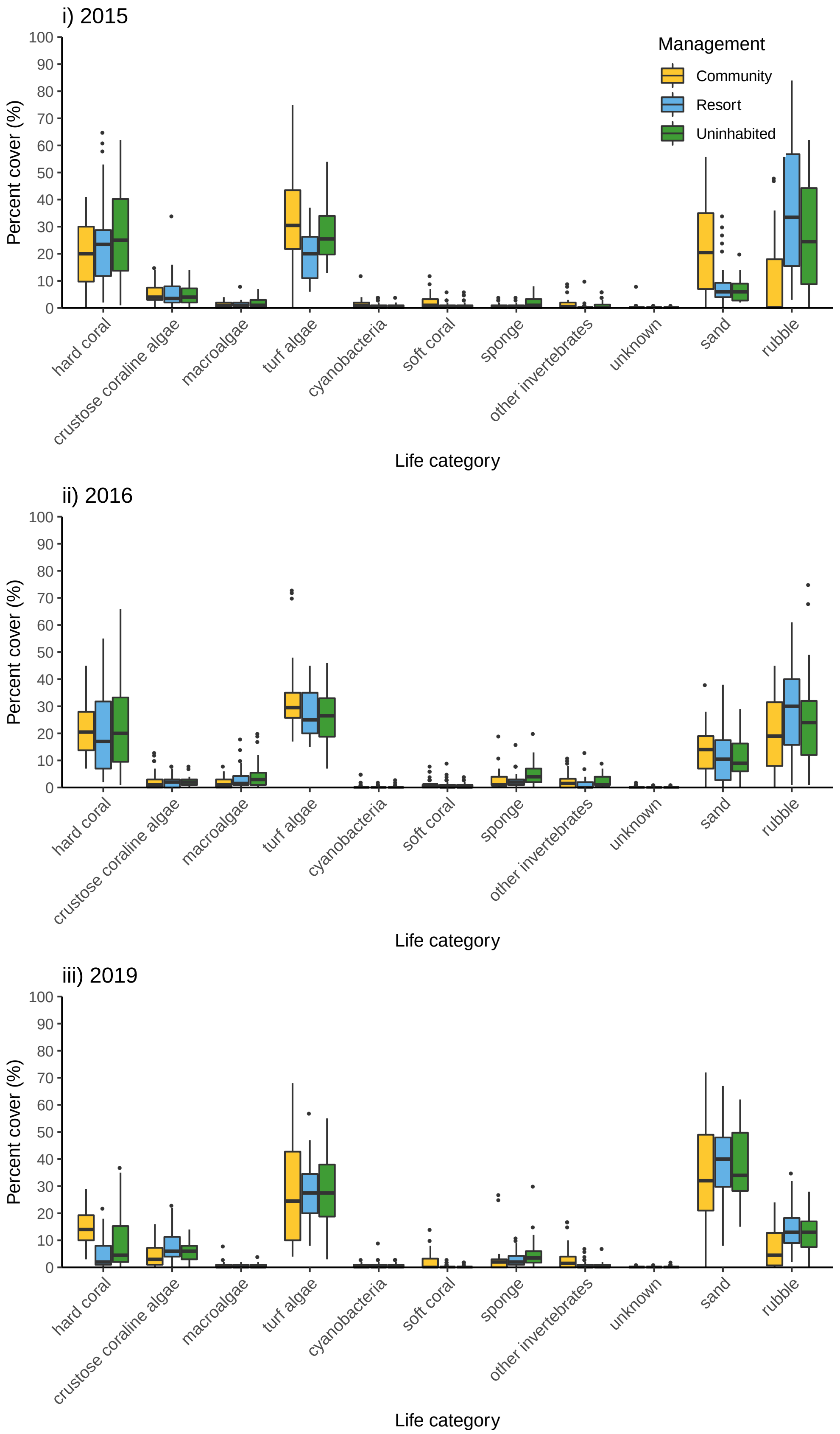


Figure 3. Percent cover of benthic organisms on reefs grouped under management regimes (uninhabited, resort and community islands) in i) 2015, ii) 2016 and iii) 2019.

Table 2. Median percent cover and interquartile range of benthic categories from point intercept surveys.

	2015						2016						2019					
	Community		Resort		Uninhabited		Community		Resort		Uninhabited		Community		Resort		Uninhabited	
	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
Hard Coral	20.0	9.8, 30.0	23.5	11.8, 28.8	25.0	13.8, 40.3	20.5	13.8, 28.0	17.0	7.0, 31.8	20.0	9.5, 33.3	14.0	10.0, 19.3	2.0	1.0, 8.0	4.5	2.0, 15.3
CCA	4.0	3.0, 7.5	3.5	2.0, 8.0	4.0	2.0, 7.3	1.0	0.0, 3.0	2.0	0.0, 3.0	2.0	1.0, 3.0	3.0	1.0, 7.3	6.0	4.0, 11.3	6.0	3.0, 8.0
Macroalgae	1.0	0.0, 2.0	1.0	0.8, 2.0	1.0	0.0, 3.0	1.0	0.0, 3.0	1.5	1.0, 4.3	3.0	1.0, 5.5	0.0	0.0, 1.0	0.0	0.0, 1.0	0.0	0.0, 1.0
Turf algae	30.5	21.8, 43.5	20.0	11.0, 26.3	25.5	19.8, 34.0	29.5	25.8, 35.0	25.0	20.0, 35.0	26.5	18.0, 33.0	24.5	10.0, 42.3	27.5	20.0, 34.5	27.5	18.8, 38.0
Cyanobacteria	1.0	0.0, 2.0	0.0	0.0, 1.0	0.0	0.0, 1.0	0.0	0.0, 0.0	0.0	0.0, 0.0	.0	0.0, 0.0	0.0	0.0, 1.0	0.0	0.0, 1.0	0.0	0.0, 1.0
Soft coral	1.0	0.0, 3.3	0.0	0.0, 1.0	0.0	0.0, 1.0	1.0	0.0, 1.0	0.0	0.0, 1.0	0.0	0.0, 1.0	0.0	0.0, 3.3	0.0	0.0, 0.0	0.0	0.0, 0.0
Sponge	0.0	0.0, 1.0	0.0	0.0, 1.0	1.0	0.0, 3.3	1.0	1.0, 4.0	2.0	1.0, 3.0	4.0	2.0, 7.0	2.0	0.0, 3.0	2.0	1.0, 4.3	3.5	1.8, 6.0
Other invertebrates	0.5	0.0, 2.0	0.0	0.0, 0.0	0.0	0.0, 1.3	1.5	0.0, 3.3	0.0	0.0, 2.0	1.0	1.0, 4.0	1.5	0.0, 4.0	0.0	0.0, 1.0	0.0	0.0, 1.0
Sand	20.5	7.0, 35.0	6.0	4.0, 9.3	6.0	2.8, 9.0	14.0	7.0, 19.0	10.5	2.8, 17.5	9.0	6.0, 16.3	32.0	21.0, 49.0	40.0	29.8, 48.0	34.0	28.3, 49.8
Rubble	0.0	0.0, 18.0	33.5	15.5, 56.8	24.5	8.8, 44.3	19.0	8.0, 31.5	30.0	15.8, 40.0	24.0	12.0, 32.0	4.5	0.8, 12.8	13.0	9.0, 18.3	13.0	7.5, 17.0

3.1.1. Uncalibrated coral cover and changes in coral cover since 2015

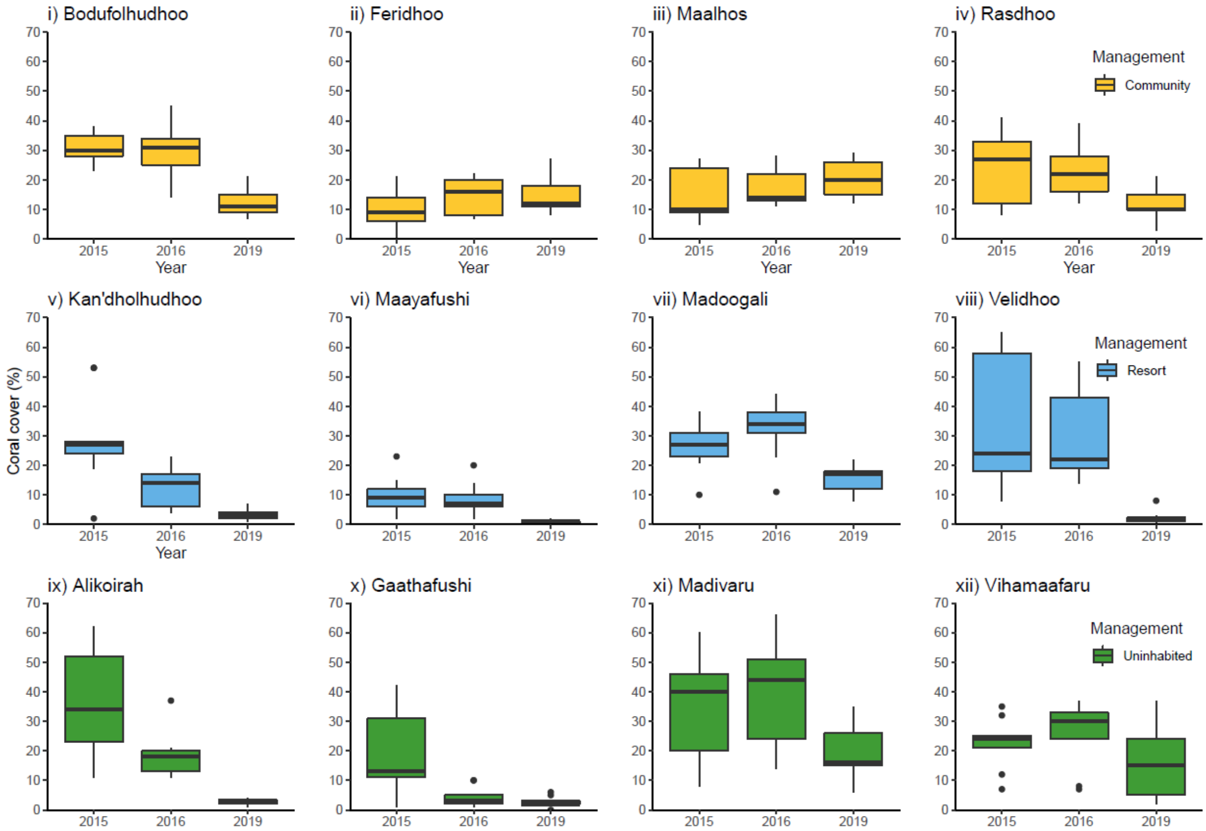


Figure 4. Coral cover at each island in 2015, 2016 and 2019. Coral cover data is presented as the raw data, i.e. not calibrated for the availability of suitable substrate that was not covered by sand.

Table 3. Median and interquartile range (IQR) percent cover of hard coral at islands under different management regimes. Data from point intercept surveys.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	30	28, 35	31	25, 34	11	9, 15
	Feridhoo	9	6, 14	16	8, 20	12	11, 18
	Maalhos	10	9, 24	14	13, 22	20	15, 26
	Rasdhoo	27	12, 33	22	16, 28	10	10, 15
Resort	Kan'dholhudhoo	27	24, 28	14	6, 17	3	2, 4
	Maayafushi	9	6, 12	7	6, 10	1	0, 1
	Madoogali	27	23, 31	34	31, 38	17	12, 18
	Velidhoo	24	18, 58	22	19, 43	2	1, 2
Uninhabited	Alikoirah	34	23, 52	18	13, 20	3	2, 3
	Gaathafushi	13	11, 31	3	2, 5	2	2, 3
	Madivaru	40	20, 46	44	24, 51	16	15, 26
	Vihamaafaru	24	21, 25	30	24, 33	15	5, 24

Community Island reefs

Coral cover declined at two of the community islands and remained relatively stable at the other two community island reefs between 2015 and 2016. The coral cover in 2015 was relatively high at Bodufolhudhoo and Rasdhoo in 2015). Coral cover remained similar in 2016 at both island reefs, however, in 2019 coral cover declined by a median of 20 % at Bodufolhudhoo and 12 % at Rasdhoo.

Coral cover at Feridhoo remained relatively stable across the three survey years, fluctuating between a median low of 9 % (IQR 6 % – 14 %) in 2015 and high of 16 % (IQR 8 % – 20 %) in 2016. Maalhos was the only island where coral cover increased each survey year, improving from a median of 10 % (IQR 9 % – 24 %) in 2015 to a median of 20 % (IQR 15 % – 26 %) in 2019.

Resort Island reefs

The coral cover at the resort island reefs of Kan'dholhudhoo, Madoogali and Velidhoo was similar in 2015. The highest coral cover observed on any transect from all the survey years was 65 % at Velidhoo. The coral cover at Maayafushi was considerably lower than at the other resort island reefs

At Kan'dholhudhoo, COTS were observed in 2016 and coral cover was lower than in 2015, declining by a median of 13 %. Coral cover at Velidhoo in 2016 was similar to 2015. In 2016 a minor increase of a median 7 % coral cover was observed at Madoogali. Coral cover at Maayafushi remained similar to 2015 in 2016.

In 2019, coral cover had declined at all resort island reefs relative to coral cover observed in 2015 and 2016, and was less than 5 % at Kan'dholhudhoo, Maayafushi and Velidhoo, whilst moderate coral cover remained at Madoogali this had also declined 17 % compared to 2016 levels.

Uninhabited Island reefs

Coral cover was relatively high in 2015 at Alikoirah, Madivaru and Vihamaafaru (Figure 4). At Gaathafushi where a high number of COTS were recorded, coral cover was lower in 2015 and

2016. The coral cover declined by a median of 14 % at Alikoirah in 2016, where COTS were also observed. Coral cover did not change considerably at either Madivaru or Vihamaafaru in 2016.

Coral cover in 2019 had declined to the lowest levels recorded at Alikoirah (median 3 %, IQR 2 % – 3 %), Madivaru (median 16 %, IQR 15 % – 26 %). Coral cover also declined at Vihamaafaru in 2019 (median 15 %, IQR 5 % – 24 %) but was more variable with some sites retaining relatively high coral cover. Coral cover remained low at Gaathafushi in 2019 (median 2 %, IQR 2 % – 3 %) with no change relative to 2016.

3.1.2. Cover of turf algae and changes since 2015

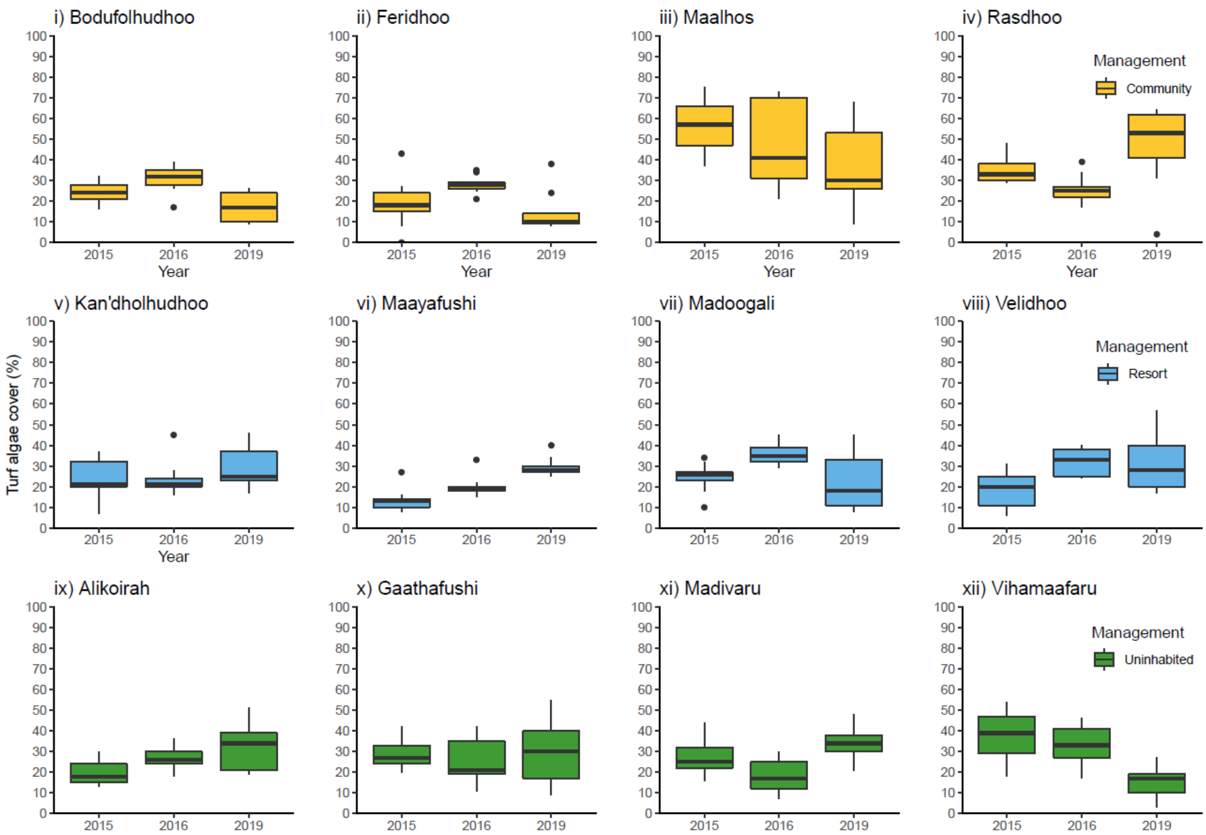


Figure 5. Percent cover of turf algae at each island in 2015, 2016 and 2019. Turf algae cover data is presented as the raw data, i.e. not calibrated for the availability of suitable substrate that was not covered by sand.

Table 4. Median and interquartile range (IQR) percent cover of turf algae at islands under different management regimes. Data from point intercept surveys.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	24	21, 28	32	28, 35	17	10, 24
	Feridhoo	18	15, 24	28	26, 29	10	9, 14
	Maalhos	57	47, 66	41	31, 70	30	26, 53
	Rasdhoo	33	30, 38	25	22, 27	53	41, 62
Resort	Kan'dholhudhoo	21	20, 32	21	20, 24	25	23, 37
	Maayafushi	13	10, 14	19	18, 20	28	27, 30
	Madoogali	26	23, 27	35	32, 39	18	11, 33
	Velidhoo	20	11, 25	33	25, 38	28	20, 40
Uninhabited	Alikoirah	18	15, 24	26	24, 30	34	21, 39
	Gaathafushi	27	24, 33	21	19, 35	30	17, 40
	Madivaru	25	22, 32	17	12, 25	34	30, 38
	Vihamaafaru	39	29, 47	33	27, 41	17	10, 19

Community Island Reefs

The cover of turf algae was relatively high but showed considerable variation between reefs and years. The cover of turf algae in 2015 was moderate at Bodufolhudhoo and Feridhoo. In 2016, turf algae cover increased at both Bodufolhudhoo (median increase 8 %) and Feridhoo (median increase 10 %). The cover of turf algae then decreased considerably at both islands by 2019. At Bodufolhudhoo median decline of 15 % and Feridhoo median decline of 18 %.

The cover of turf algae was very high at Maalhos in 2015 (median 57 %, IQR 47 % – 66 %) and although it had declined at several transects in 2016 and in 2019, it remained high (median 30 %, IQR 26 % – 53 %) by the end of the surveys.

The cover of turf algae was also high at Rasdhoo in 2015 (median 33 %, IQR 30 % – 38 %), and although cover of turf algae had declined slightly in 2016, the cover of turf algae was very high in 2019 (median 53 %, IQR 41 % – 62 %).

Resort Island Reefs

Turf algae cover did not follow a uniform pattern across resort islands, one island increased each year, one island remained relatively stable and had notable increases and decrease over the three years (Figure 5). The cover of turf algae in 2015 was moderate at Kan'dholhudhoo, Maayafushi, Madoogali and Velidhoo.

The cover of turf algae increased at three resort islands between 2015 and 2016, Maayafushi (median increase 6 %), Madoogali (median increase 9 %) and Velidhoo (median increase 13 %). Whilst cover of turf algae remained similar at Kan'dholhudhoo. In 2019, the cover of turf algae was generally high at resort island reefs. At Kan'dholhudhoo and Madoogali, turf algae cover was similar to 2015. Whilst turf algae cover was higher relative to 2015 at Maayafushi and Velidhoo.

Uninhabited Island Reefs

Turf algae cover was relatively high at uninhabited island reefs across all survey years, median cover was greater than 15 % across all islands and years surveys (Table 4). Percent cover of turf algae was similar between 2015 and 2016 for all uninhabited island reefs. A minor increase of median 8 % in turf algae was observed at Alikoirah and a minor decrease in turf algae cover of median 8 % was observed at Madivaru. Whilst the turf algae cover remained almost the same from 2015 to 2016 at Gaathafushi and Vihamaafaru.

The turf algae increased further by a median of 8 % in 2019 at Alikoirah and increased by a median of 9 % at Gaathafushi 17 % at Madivaru. Meanwhile cover of turf algae declined by a median of 16 % at Vihamaafaru.

3.1.3. Cover of crustose coralline algae and changes since 2015

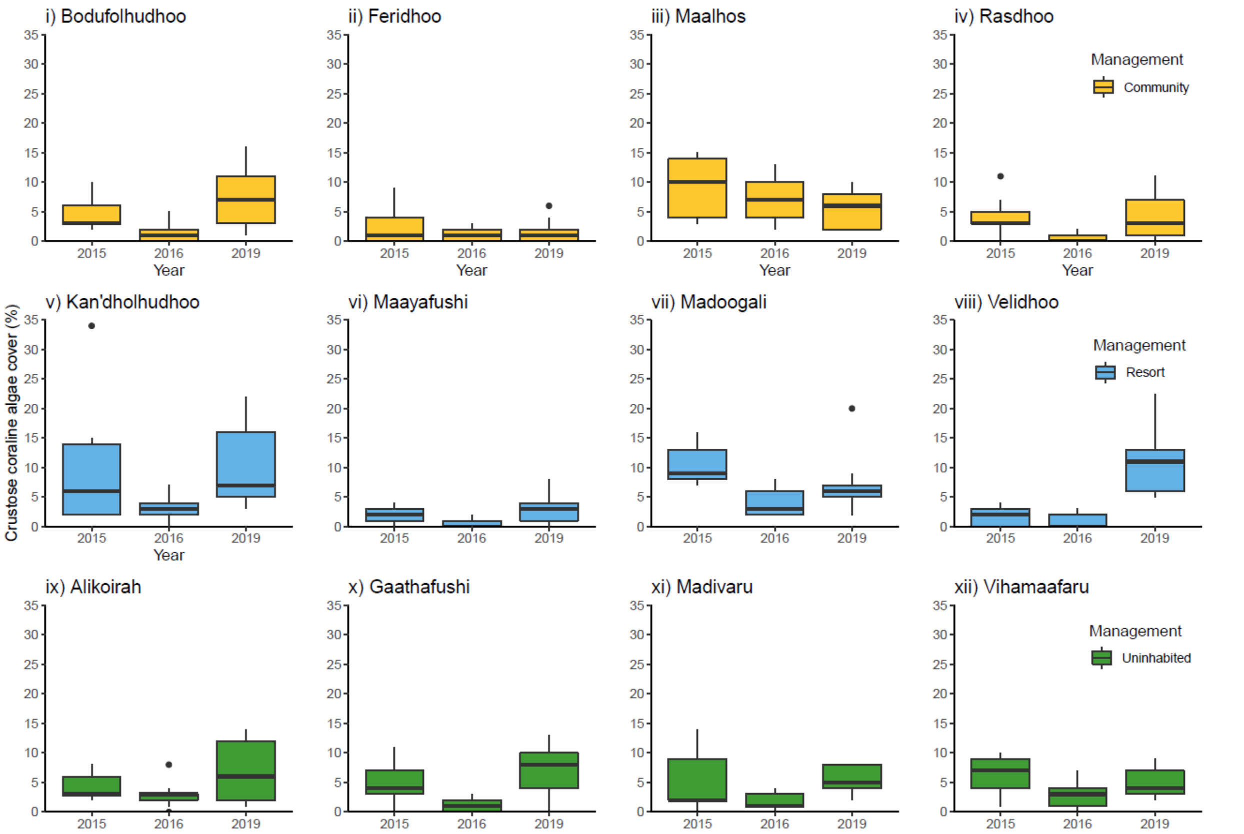


Figure 6. Percent cover of crustose coralline algae at each island in 2015, 2016 and 2019. Percent cover data is presented as the raw data, i.e. not calibrated for the availability of suitable substrate that was not covered by sand.

Table 5. Median and interquartile range (IQR) percent cover of crustose coralline algae at islands under different management regimes. Data from point intercept surveys.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	3	3, 6	1	0, 2	7	3, 11
	Feridhoo	1	0, 4	1	0, 2	1	0, 2
	Maalhos	10	4, 14	7	4, 10	6	2, 8
	Rasdhoo	3	3, 5	0	0, 1	3	1, 7
Resort	Kan'dholhudhoo	6	2, 14	3	2, 4	7	5, 16
	Maayafushi	2	1, 3	0	0, 1	3	1, 4
	Madoogali	9	8, 13	3	2, 6	6	5, 7
	Velidhoo	2	0, 3	0	0, 2	11	6, 13
Uninhabited	Alikoirah	3	3, 6	3	2, 3	6	2, 12
	Gaathafushi	4	3, 7	1	0, 2	8	4, 10
	Madivaru	2	2, 9	1	1, 3	5	4, 8
	Vihamaafaru	7	4, 9	3	1, 4	4	3, 7

Community Island Reefs

3.1.4. The cover of CCA was generally low across community island reefs in 2015 and 2016, only one island had CCA cover greater than 3 % (Figure 6,

Table 5).

The cover of CCA declined at all islands between 2015 and 2016. In 2019, cover of CCA increased by a median of 6 % at Bodufolhudhoo (median 7 %, IQR 3 % – 11 %), remained low at Feridhoo (median 1 %, IQR 0 % – 2 %), moderate at Maalhos (median 6 %, IQR 2 % – 8 %) and increased slightly at Rasdhoo (median 3 %, IQR 1 % – 7 %).

Resort Island Reefs

3.1.5. The cover of CCA was moderate in 2015, decreased in 2016 and then by 2019 had increased back to 2015 levels at three reefs and to more than five times 2015 levels at one reef (

Table 5). In 2015, the cover of CCA was low at Maayafushi and Velidhoo and was moderate at Kan'dholhudhoo and Madoogali. The cover of CCA declined at all islands in 2016. In 2019, the cover of CCA had increased at resort island reefs Kan'dholhudhoo, Maayafushi, Madoogali (median 6 %, IQR 5 % – 7 %) and Velidhoo. However only at Velidhoo was cover of CCA

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	3	3, 6	1	0, 2	7	3, 11
	Feridhoo	1	0, 4	1	0, 2	1	0, 2
	Maalhos	10	4, 14	7	4, 10	6	2, 8
	Rasdhoo	3	3, 5	0	0, 1	3	1, 7
Resort	Kan'dholhudhoo	6	2, 14	3	2, 4	7	5, 16
	Maayafushi	2	1, 3	0	0, 1	3	1, 4
	Madoogali	9	8, 13	3	2, 6	6	5, 7
	Velidhoo	2	0, 3	0	0, 2	11	6, 13
Uninhabited	Alikoirah	3	3, 6	3	2, 3	6	2, 12
	Gaathafushi	4	3, 7	1	0, 2	8	4, 10
	Madivaru	2	2, 9	1	1, 3	5	4, 8
	Vihamaafaru	7	4, 9	3	1, 4	4	3, 7

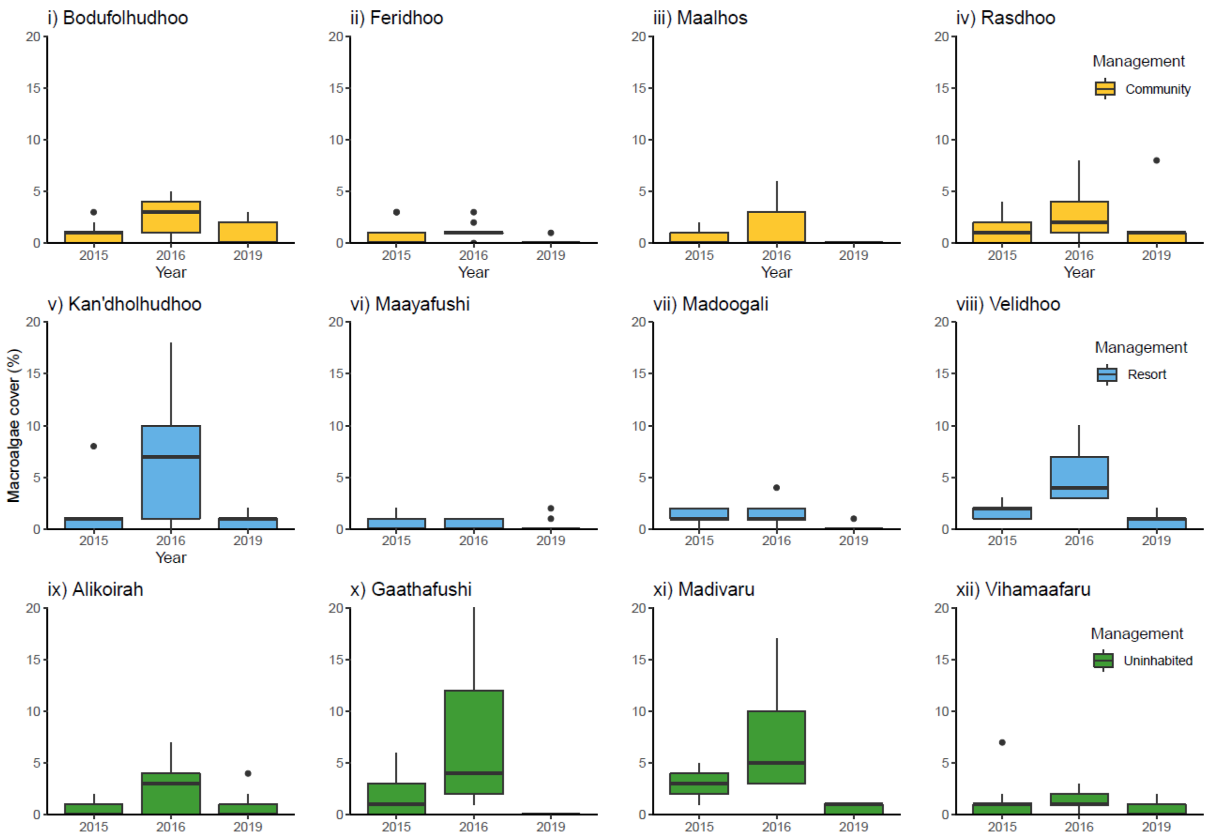
greater relative to 2015.

Uninhabited Island Reefs

3.1.6. The cover of CCA approximately doubled at 3 uninhabited island reefs, and declined slightly at the other, between 2015 and 2019 (Figure 6). The cover of CCA was moderate in 2015 at Alikoirah, Gaathafushi, Madivaru and Vihamaafaru (

Table 5). In 2016, the cover of CCA had dropped to lower levels than those observed in 2015 at Gaathafushi, Madivaru, and Vihamaafaru. In 2019, the cover of CCA was double the cover observed in 2015, at Alikoirah (median 6 %, IQR 2 % – 12 %), Gaathafushi (median 8 %, IQR 4 % – 10 %) and Madivaru (median 5 %, IQR 4 % – 8 %) and remained stable at Vihamaafaru (median 4 %, IQR 3 % – 7 %).

3.1.7. Cover of macroalgae and changes since 2015



Madivaru	2	2, 9	1	1, 3	5	4, 8

Figure 7. Percent cover of macroalgae at each island in 2015, 2016 and 2019. Percent cover data is presented as the raw data, i.e. not calibrated for the availability of suitable substrate that was not covered by sand.

Table 6. Median and interquartile range (IQR) percent cover of macroalgae at islands under different management regimes. Data from point intercept surveys.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	1	0, 1	3	1, 4	0	0, 2
	Feridhoo	0	0, 1	1	1, 1	0	0, 0
	Maalhos	0	0, 1	0	0, 3	0	0, 0
	Rasdhoo	1	0, 2	2	1, 4	1	0, 1
Resort	Kan'dholhudhoo	1	0, 1	7	1, 10	1	0, 1
	Maayafushi	0	0, 1	0	0, 1	0	0, 0
	Madoogali	1	1, 2	1	1, 2	0	0, 0
	Velidhoo	2	1, 2	4	3, 7	1	0, 1
Uninhabited	Alikoirah	0	0, 1	3	0, 4	0	0, 1
	Gaathafushi	1	0, 3	4	2, 12	0	0, 0
	Madivaru	3	2, 4	5	3, 10	1	0, 1
	Vihamaafaru	1	0, 1	1	1, 2	0	0, 1

Community Island Reefs

The cover of macroalgae was generally low at community island reefs in 2015 but increased at Bodufolhudhoo and Maalhos in 2016 and by 2019 had returned to similar levels as 2015 (Figure 7). In 2015, macroalgae cover was very low at Bodufolhudhoo and Rasdhoo, both had a median cover of 1 % (IQR 0 % – 1 %), and macroalgae was rarely observed at both Feridhoo and Maalhos (Table 6). In 2016, macroalgae cover had increased by a median of 2 % at Bodufolhudhoo, and 1 % at both Feridhoo and Rasdhoo. Macroalgae cover remained rare at Maalhos in 2016. Macroalgae were rare in at all reefs in 2019, Rasdhoo (median 1 %, IQR 0 % – 1 %) was the only island where median cover was not 0 %.

Resort Island Reefs

The cover of macroalgae was generally low at resort island reefs in 2015 but increased at Kan'dholhudhoo and Velidhoo in 2016 and by 2019 had returned to similar levels as 2015. In 2015, macroalgae were rare at Kan'dholhudhoo, Maayafushi and very low at Madoogali and Velidhoo. In 2016, macroalgae cover had increased by a median of 6 % at Kan'dholhudhoo and 2 % at Velidhoo. Macroalgae were rare again in 2019 and macroalgae cover was very low at Kan'dholhudhoo (median 1 %, IQR 0 % – 1 %) and Velidhoo (median 1 %, IQR 0 % –

1 %), and rarely observed at Maayafushi (median 0 %, IQR 0 % – 0 %) and Madoogali (median 0 %, IQR 0 % – 0 %).

<u>Uninhabited Island Reefs</u>

The cover of macroalgae was generally low at uninhabited islands in 2015, increased in 2016 at all the islands, and by 2019 had declined to levels below 2015 at three of the islands. In 2015 macroalgae were rare at Alikoirah, and their cover was very low at Gaathafushi, and Vihamaafaru and low at Madivaru. In 2016 macroalgae cover had generally increased at Alikoirah, Gaathafushi and, Madivaru and macroalgae were more frequently observed at Vihamaafaru (median 1 %, IQR 1 % – 2 %). Macroalgae cover had declined by 2019 and were now rare at Alikoirah (median 0 %, IQR 0 % – 1 %), Madivaru (median 1 %, IQR 0 % – 1 %) and Vihamaafaru (median 0 %, IQR 0 % – 1 %). Whilst no macroalgae were recorded at Gaathafushi (median 0 %, IQR 0 % – 0 %).

3.1.8. Cover of sponges and changes since 2015

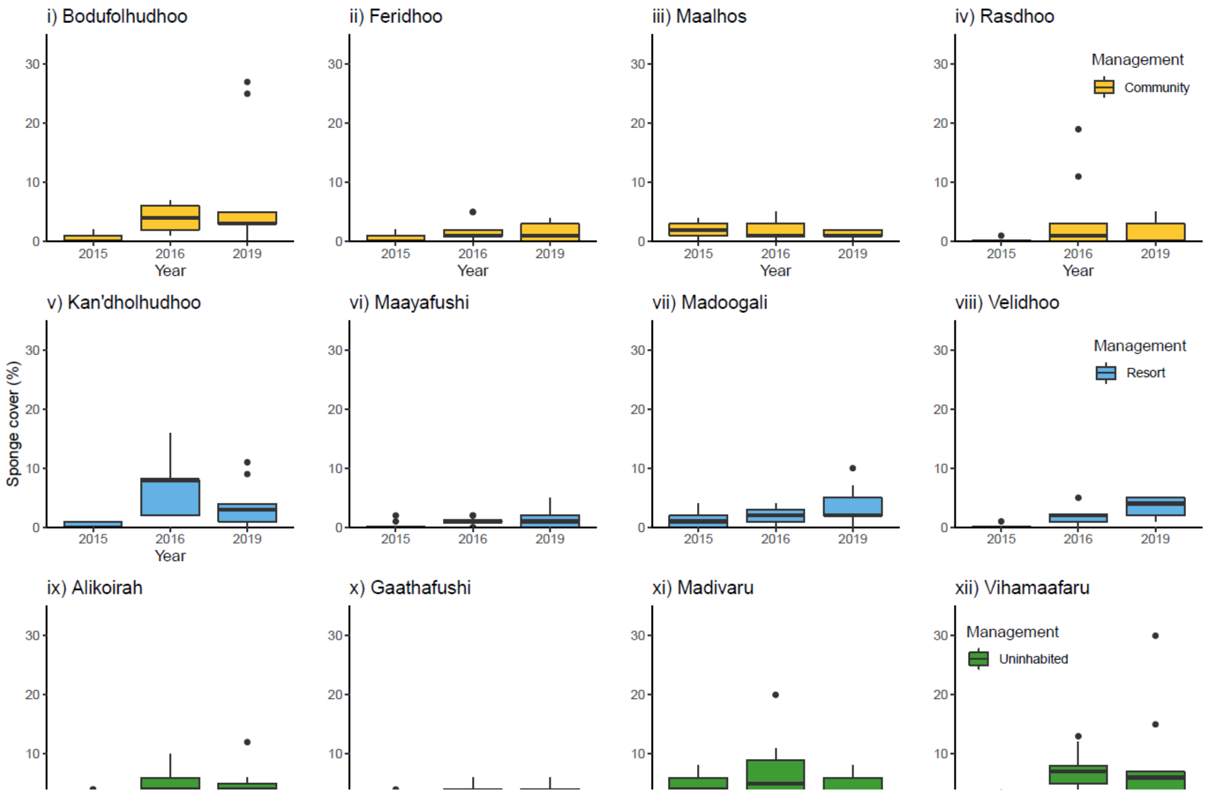


Figure 8. Percent cover of sponge at each island in 2015, 2016 and 2019. Percent cover data is presented as the raw data, i.e. not calibrated for the availability of suitable substrate that was not covered by sand.

Table 7. Median and interquartile range (IQR) percent cover of sponge at islands under different management regimes. Data from point intercept surveys.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	0	0, 1	4	2, 6	3	3, 5
	Feridhoo	0	0, 1	1	1, 2	1	0, 3
	Maalhos	2	1, 3	1	1, 3	1	1, 2
	Rasdhoo	0	0, 0	1	0, 3	0	0, 3
Resort	Kan'dholhudhoo	0	0, 1	8	2, 8	3	1, 4
	Maayafushi	0	0, 0	1	1, 1	1	0, 2
	Madoogali	1	0, 2	2	1, 3	2	2, 5
	Velidhoo	0	0, 0	2	1, 2	4	2, 5
Uninhabited	Alikoirah	1	0, 1	4	3, 6	4	2, 5
	Gaathafushi	0	0, 1	2	1, 4	2	2, 4
	Madivaru	4	0, 6	5	2, 9	3	1, 6
	Vihamaafaru	2	1, 3	7	5, 8	6	3, 7

Community Island Reefs

The cover of sponges was very low at all community islands in 2015 and small increases were observed at three of these islands between 2015 and 2019 (Figure 8). Sponges were rarely encountered in 2015 at Bodufolhudhoo, Feridhoo or Rasdhoo and cover was very low at Maalhos (Table 7). Sponge cover remained low, but sponges were more frequently observed in 2016 at all four islands. The cover of sponges in 2019 remained similar to 2016 for most community island reefs, though sponges became scarcer at Rasdhoo.

Resort Island Reefs

The cover of sponges was very low in 2015, increased by 2016 and remained similar to 2016 in 2019 at all resort island reefs. Sponges were rarely observed at any of the resort island reefs in 2015. Sponge cover increased to low levels in 2016 at Kan'dholhudhoo (median 8 %, IQR 2 % – 8 %), Maayafushi (median 1 %, IQR 1 % – 1 %), Madoogali (median 2.0 %, IQR 1 % – 3 %) and Velidhoo (median 2 %, IQR 1 % – 2 %). In 2019, the cover of sponges had increased further at some of the transects at Kan'dholhudhoo (max 11 %, median 3 %, IQR 1 % – 4 %). Little change was observed for Maayafushi where sponge cover remained low. Sponge cover remained similar in 2019 although increased at some transects at both Madoogali and Velidhoo.

Uninhabited Island Reefs

The cover of sponges was low in 2015 and increased in 2016 at all uninhabited island reefs. Sponge cover in 2019 was similar to 2016. In 2015, sponges were rare at Alikoirah and Gaathafushi, and low at Madivaru and Vihamaafaru. In 2016, the cover of sponges increased at all four islands and remained at similar levels in 2019 for Alikoirah (median 4 %, IQR 2 % – 5 %), Gaathafushi (median 2 %, IQR 2 % – 4 %), Madivaru (median 3 %, IQR 1 % – 6 %) and Vihamaafaru (median 6 %, IQR 3 % – 7 %).

3.2. Coral recruitment

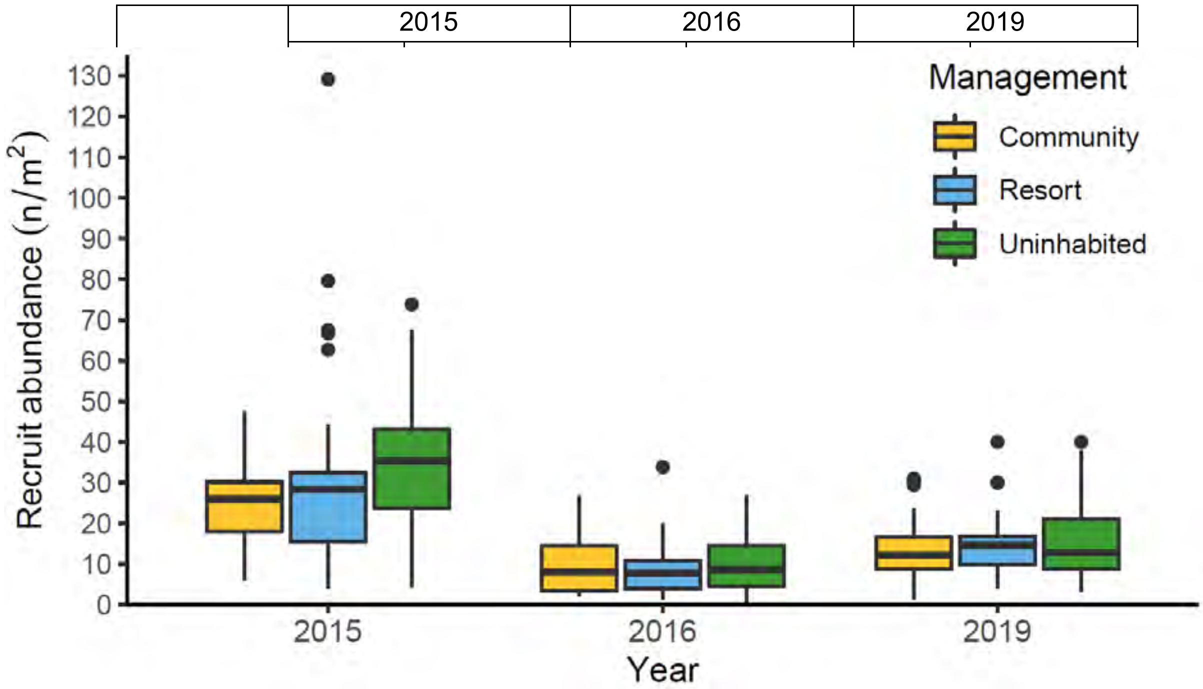


Figure 9. Coral recruit abundance observed in North Ari Atoll surveys undertaken in 2015, 2016 and 2019. The abundance of coral recruits per m2 are represented as median, quartile ranges, minimum and maximum values for each management regime.

Table 8. Median and interquartile range (IQR) of all coral recruits identified at different management regimes across the three survey years.

The total abundance of coral recruits was higher in 2015 than either 2016 or 2019 (Figure 9). Recruit abundance declined by approximately at 55 % community, 54 % at resort and 70 %on uninhabited island reefs (

Table 8) from 2015 to 2016, The resort island of Kan'dulhudhoo was the only island where declines in the abundance of coral recruits where not clear relative to 2015 because of high variability in recruit abundance along transects. There was no apparent difference between 2016 and 2019. Recruit abundance was higher on uninhabited island reefs in 2015 compared to community and resort island reefs. Recruit abundance did not differ between resort and community reefs in 2015. Recruit numbers remained lower in 2019 where no significant differences were observed in the recruit abundance between in 2016 or 2019 at any management regime. The abundance of recruits increased from 2016 to 2019 but remained approximately 51 % lower at uninhabited reefs, 28 % lower at resort reefs, and 30 % lower at community reefs relative to recruit abundances observed in 2015.

The data indicates that by 2019, a history of COTS at an island had resulted in greater declines in the abundance of coral recruits. This correlates with greater macroalgae cover following COTS disturbance. Lower coral recruitment may not result only from direct impacts of COTS on coral recruits (see section on macroalgae). COTS have impacted Alikoirah, Gaathafushi, Maayafushi and Kan'dholhudhoo to various undescribed extents since 2015. The abundance of coral recruits had declined by approximately 60 % in 2019 relative to 2015 at both Alikoirah and Gaathafushi. Recruit abundance had declined by ~ 40 % at Maayafushi in 2019 relative to 2015. Recruit abundance at Kan'dholhudhoo was variable but declined over 80% at some transects in 2016 despite similar recruit abundance observed in 2019 relative to 2015.

The recruit data collected did not identify variation in the abundance of coral recruits associated with the location of islands within North Ari Atoll (inner islands or outer islands), with local exposure of reefs (sheltered or exposed) or with reef habitats (terrace, slope or wall). During the 2015 surveys, recruits from 39 genera were recorded (Table 9). This number dropped to 34 in 2016 and to 29 by 2019. The genera missing in 2016 were *Alveopora, Mussidae, Plerogyra, Podabacia* and *Tubastraea*. The five additional genera absent in 2019 were *Acanthastrea, Coscinaraea, Diploastrea, Merulina* and *Symphyllia*.

Table 9. Coral genera recorded on belt transect surveys for recruits and adults (larger than 6 cm diameter) and point intercept transect (PIT) surveys

	Recruit (belt transects)			Adults (belt transects)			PIT		
Genus	2015	2016	2019	2015	2016	2019	2015	2016	2019
Acanthastrea	X	X		X	X		X	X	
Acropora	X	X	X	X	X	X	X	X	X
Alveopora	X			X	X			X	
Astreopora	X	X	X	X	X	X	X	X	X
Coscinaraea	X	X		X	X	X			
Cyphastrea	X	X	X	X	X	X	X	X	X
Diploastrea	X	X		X	X	X	X	X	X
Echinopora	X	X	X	X	X	X	X	X	X
Favia	X	X	X	X	X	X	X	X	X
Favites	X	X	X	X	X	X	X	X	X
Fungia	X	X	X	X	X	X	X	X	X
Galaxea	X	X	X	X	X	X	X	X	X
Gardineroseris	X	X	X	X	X	X	X	X	X
Goniastrea	X	X	X	X	X	X	X	X	X
Goniopora	X	X	X	X	X	X	X	X	X
Halomitra	X	X	X	X	X	X		X	
Hydnophora	X	X	X	X	X	X	X	X	X
Leptastrea	X	X	X	X	X	X	X		
Leptoseris	X	X	X	X	X	X	X	X	X
Lobophyllia	X	X	X	X	X	X	X	X	X
Merulina	X	X		X	X	X	X	X	X
Montastraea	X	X	X	X	X	X			
Montipora	X	X	X	X	X	X	X	X	X
Mussidae	X								
Mycedium	X	X	X	X	X		X		
Oxypora	X	X	X	X	X	X		X	X
Pachyseris	X	X	X	X	X	X	X	X	X
Pavona	X	X	X	X	X	X	X	X	X
Pectinia	X	X	X	X	X	X		X	X
Physogyra	X	X	X	X	X	X		X	
Platygyra	X	X	X	X	X	X	X	X	X
Plerogyra	X					X			
Pocillopora	X	X	X	X	X	X	X	X	X
Podabacia	X			X	X	X			

Porites	X	X	X	X	X	X	X	X	X
Psammocora	X	X	X	X	X	X	X	X	X
Symphyllia	X	X		X	X	X			
Tubastraea	X			X		X			
Turbinaria	X	X	X	X	X	X	X		
Count:	39	34	29	37	36	35	35	38	30

3.3. Most commonly observed coral genera (Acropora, Pocillopora, Porites and Pavona)

3.3.1. Coral genera observed in 2015, 2016 and 2019

The PIT surveys of North Ari Atoll recorded 35 genera of coral in 2015, 38 in 2016 and 30 in 2019 (Table 10) The genus with highest overall in 2015 and 2016 cover was *Acropora,* followed by *Porites* and *Pocillopora* (Table 10). In 2015 the genera *Pocillopora*, *Psammocora, Pavona*, *Montipora*, *Leptoseris*, *Goniastrea*, and *Favites*, were also recorded more frequently than other coral genera. In 2016 the genera *Pocillopora*, *Pavona*, *Leptoseris*, *Fungia* and *Favites* were also observed more frequently than other coral genera. In 2019, coral cover was exceptionally low (discussed in section 3.1.1**Error! Reference source not found.**) and fewer colonies of corals were observed. The genera *Porites* and *Acropora* remained the most frequently recorded. The genera *Favites*, *Psammocora*, *Leptoseris* and *Pocillopora* were also observed more frequently than other coral genera.

The following 9 genera were not recorded in PIT surveys undertaken in 2019 but were observed in 2016- *Physogyra*, *Millepora*, *Leptoria*, *Halomitra*, *Echinophyllia*, *Dendrophyllia*, *Ctenactis*, *Alveopora*, and *Acanthastrea*. Whilst the following 5 genera were observed in 2015 and not subsequently- *Pleurogyra*, *Leptastrea*, *Mycedium*, *Heliopora* and Euphyllia.

Table 10. Median percent cover and interquartile range (IQR) of coral general observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

	2015		2016		2019	
Genus	Median	IQR	Median	IQR	Median	IQR
Acanthastrea	0	0, 0	0	0, 0	0	0, 0
Acropora	8	2, 20	5	2, 12	1	0, 2
Alveopora	0	0, 0	0	0, 0	0	0, 0
Astreopora	0	0, 0	0	0, 0	0	0, 0
Cyphastrea	0	0, 0	0	0, 0	0	0, 0
Diploastrea	0	0, 0	0	0, 0	0	0, 0
Echinopora	0	0, 0	0	0, 0	0	0, 0
Favia	0	0, 0	0	0, 0	0	0, 0
Favites	0	0, 1	0	0, 1	0	0, 1
Fungia	0	0, 0	0	0, 1	0	0, 0
Galaxea	0	0, 0	0	0, 0	0	0, 0
Gardineroseris	0	0, 0	0	0, 0	0	0, 0
Goniastrea	0	0, 1	0	0, 0	0	0, 0
Goniopora	0	0, 0	0	0, 0	0	0, 0
Halomitra	0	0, 0	0	0, 0	0	0, 0
Hydnophora	0	0, 0	0	0, 0	0	0, 0
Leptastrea	0	0, 0	0	0, 0	0	0, 0
Leptoseris	0	0, 1	0.5	0, 2	0	0, 1
Lobophyllia	0	0, 0	0	0, 0	0	0, 0
Merulina	0	0, 0	0	0, 0	0	0, 0
Montastrea	0	0, 0	0	0, 0	0	0, 0
Montipora	0	0, 1	0	0, 0	0	0, 0
Mycedium	0	0, 0	0	0, 0	0	0, 0
Oxypora	0	0, 0	0	0, 0	0	0, 0
Pachyseris	0	0, 0	0	0, 0	0	0, 0
Pavona	0	0, 1	0	0, 1	0	0, 0
Pectinia	0	0, 0	0	0, 0	0	0, 0
Physogyra	0	0, 0	0	0, 0	0	0, 0
Platygyra	0	0, 0	0	0, 0	0	0, 0
Plerogyra	0	0, 0	0	0, 0	0	0, 0
Pocillopora	1	0, 2	1	0, 2	0	0, 1
Porites	3	1, 5	3.5	1, 7	2	0, 4
Psammocora	0	0, 1	0	0, 0	0	0, 1
Symphillia	0	0, 0	0	0, 0	0	0, 0
Tubastrea	0	0, 0	0	0, 0	0	0, 0
Turbinaria	0	0, 0	0	0, 0	0	0, 0

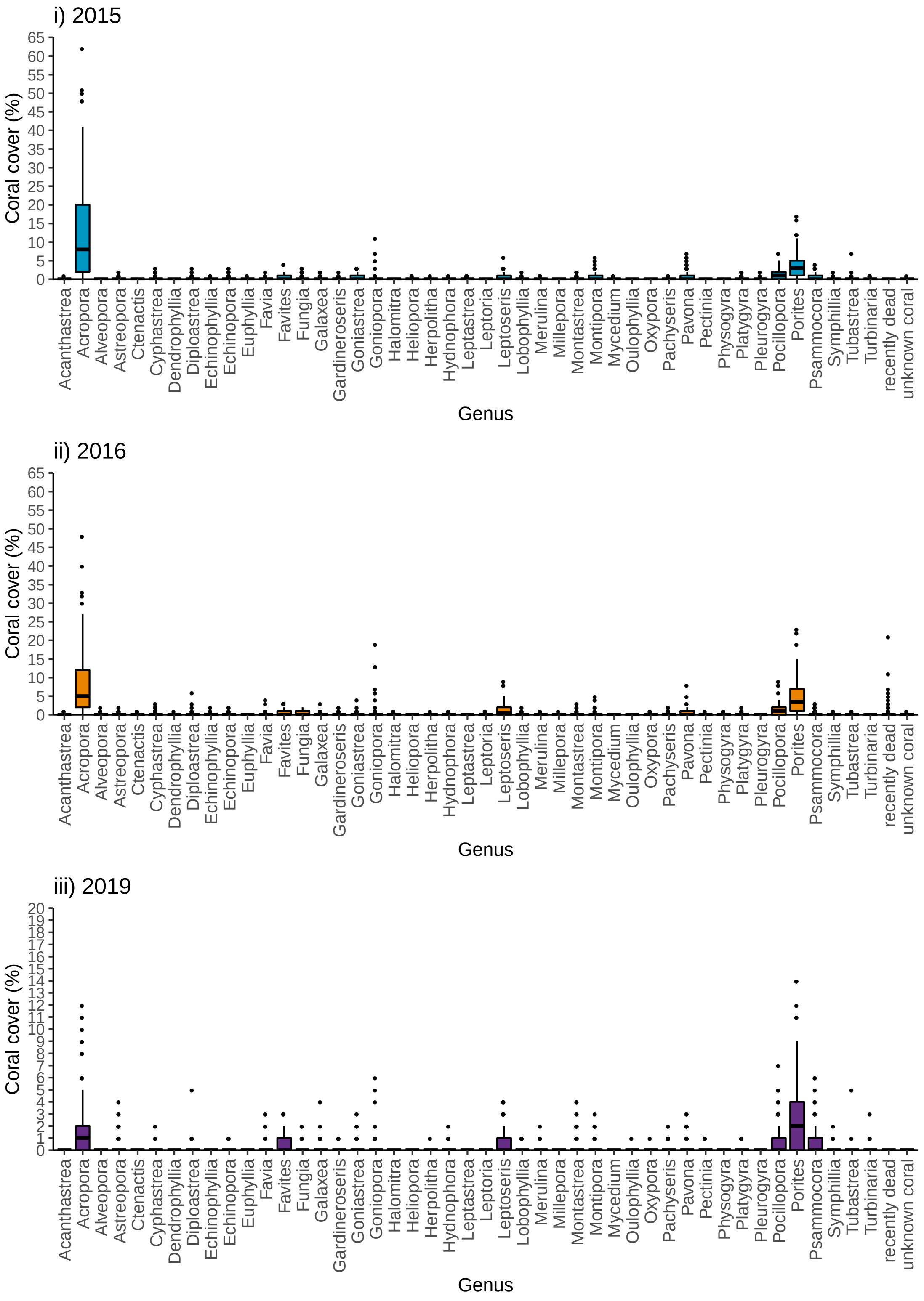


Figure 10. The percent cover of coral genera recorded in point intercept transect (PIT) surveys undertaken in i) 2015, ii) 2016 and iii) 2019. Data is presented as median and quartile ranges for 108 transects surveyed at North Ari Atoll.

3.3.2. *Acropora*

3.3.2.1. Percent cover and change in percent cover of *Acropora*

The percentage of the available substrate (calibrated to exclude sand) covered by the coral genus *Acropora* declined significantly across all sites over the three survey years (χ^2(df =2) = 71.5, p < 0.01). *Acropora* cover dropped from 2015 to 2016 by 4.8 % (±1.3 % S.E) and by a further 6.5 % (±1.3 % S.E.) in 2019. *Acropora* cover was relatively high at several of the islands surveyed in 2015, in particular the uninhabited island Alikoirah (median 25.5 %, IQR 14.6 % – 39.8 %) and the resort island Velidhoo (median 23.7 %, IQR 12.9 % – 54.3 %) (Figure 11, Table 11).

The cover of *Acropora* on available substrate declined between 2015 and 2016, at the uninhabited islands of Alikoirah, Gaathafushi, and the resort island of Kan'dholhudhoo, all which were impacted by COTS to un-described extents at some point in 2015 and 2016. The cover of *Acropora* on available substrate also declined at the two community island reefs of Bodufolhudhoo and Rasdhoo between 2015 and 2016. Between 2015 and 2016, the cover of *Acropora* on available substrate remained similar at the uninhabited island reefs of Madivaru and Vihamaafaru, at the resort island reefs of Maayafushi, Madoogali and Velidhoo and also at the community island of Feridhoo. Cover of Acropora at Maalhos, which was reported to be "noticeably degraded" in 2015, remained low, throughout the surveys.

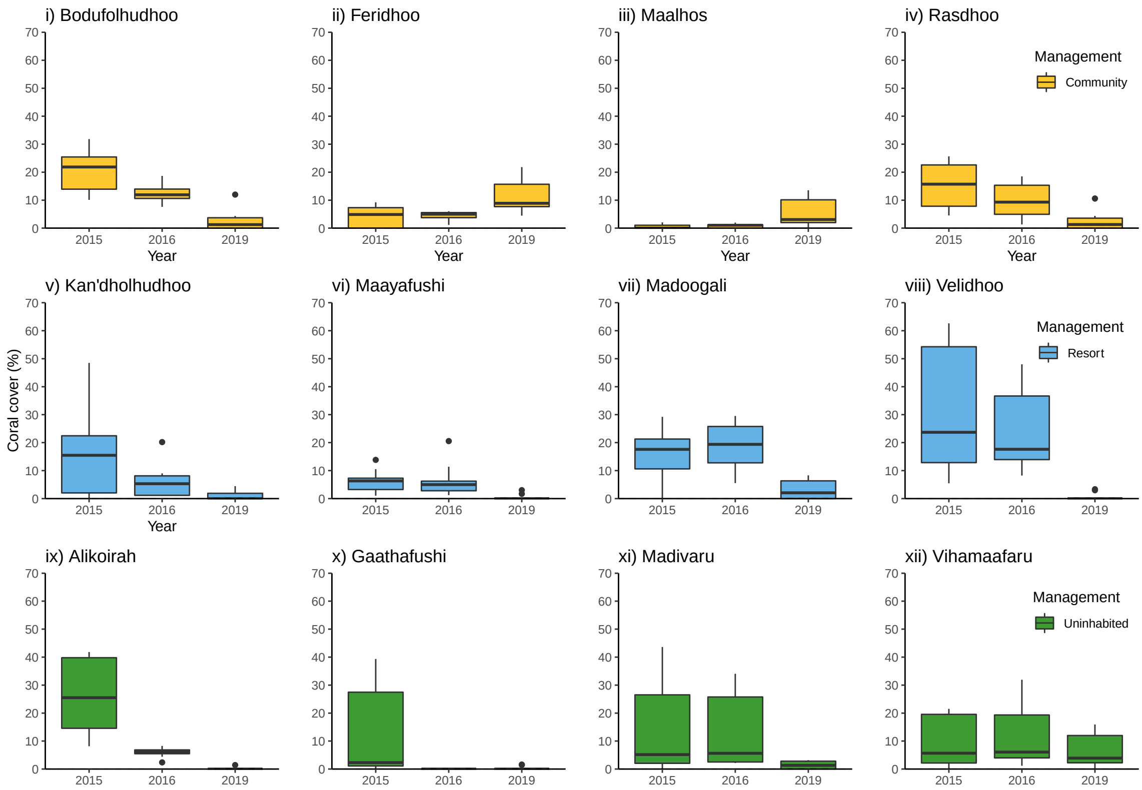


Figure 11. The percent cover of the coral genus Acropora at each island surveyed in North Ari Atoll in 2015, 2016 and 2019. Islands are ordered from left to right according to management regimes of uninhabited islands, resort islands and community islands. COTS are known to have been present at in 2015 at Alikoirah, Gaathafushi and Maayafushi, whilst also at Kan'dholhudhoo in 2016. Data is calibrated for available substrate by removing sand.

Table 11. Median percent cover and interquartile range (IQR) of *Acropora* observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	21.9	13.9, 25.4	11.9	10.6, 14	1.3	0, 3.7
	Feridhoo	4.9	0, 7.3	5	3.8, 5.6	8.9	7.7, 15.7
	Maalhos	0	0, 1.1	1	0, 1.2	3.1	2, 10.1
	Rasdhoo	15.7	7.8, 22.6	9.3	4.9, 15.3	1.3	0, 3.6
Resort	Kan'dholhudhoo	15.5	2, 22.4	5.3	1.1, 8.1	0	0, 1.9
	Maayafushi	6.3	3.2, 7.3	5	2.8, 6.3	0	0, 0
	Madoogali	17.6	10.6, 21.3	19.4	12.8, 25.8	2.1	0, 6.3
	Velidhoo	23.7	12.9, 54.3	17.6	14, 36.7	0	0, 0
Uninhabited	Alikoirah	25.5	14.6, 39.8	6.1	5.5, 6.8	0	0, 0
	Gaathafushi	2.3	1.1, 27.5	0	0, 0	0	0, 0
	Madivaru	5.2	2.1, 26.5	5.6	2.5, 25.8	1.3	0, 2.8
	Vihamaafaru	5.7	2.2, 19.5	6.1	4, 19.3	3.9	2.2, 12

3.3.2.2. Habitat distribution patterns of *Acropora*

There were significant differences in the percent cover of *Acropora* associated with management. The cover of *Acropora* was significantly higher at resort compared to community island reefs by 6.6 % (± 2.5 % S.E., df = 8.61, t = 2.60 p < 0.05. There were no other significant differences between management regimes, though *Acropora* cover was marginally, but not significantly higher, at uninhabited island reefs compared to community island reefs. The effects of management were not altered by island location (χ 2(df = 2) = 2.72, p > 0.05) or local reef exposure (χ 2(df = 2) = 2.72, p > 0.05).

The baseline surveys undertaken in 2015 suggest that *Acropora* occupy more of the available substrate on inner island reefs than on outer islands (Figure 12). *Acropora* cover was 5.3 % (± 2.5 % S.E.) higher at inner atoll reefs, though this difference was marginally non-significant (df = 9.44, t =-2.092, p = 0.06). Disturbance from the bleaching event in 2016, and resulting impacts on the cover of *Acropora*, appears to have varied in its extent according to habitat. Greater declines in the cover of Acropora may have occurred at inner island reefs relative to outer island reefs and on sheltered reefs relative to exposed reefs since 2015. Historical presence of COTS significantly impacted the cover of *Acropora.*

Reef gradient had a significant influence on the cover of *Acropora* (χ^2(df = 2) = 11.64, p < 0.01). *Acropora* cover was highest on reef slopes.

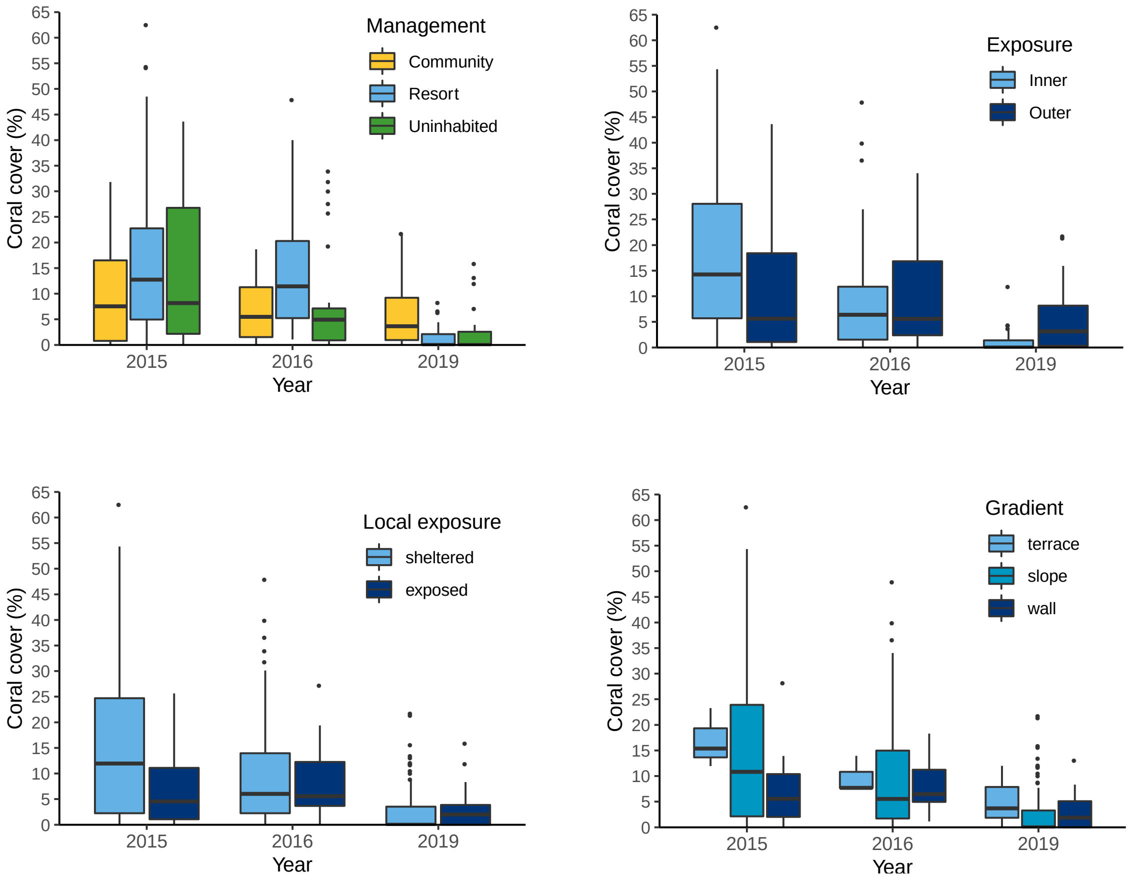


Figure 12. Percent cover of the coral genus Acropora at North Ari Atoll. Data was collected with point intercept transects and does not include recruits. Data is combined for i) management regimes of Uninhabited, Resort and Community islands, ii) Island Exposure at the Inner or Outer edge of the atoll, iii) Local exposure of the reef sites to sheltered or exposed conditions (e.g. waves, wind) and iv) The gradient of the reef of terrace, slope or wall habitat.

3.3.2.3. Recruitment patterns of *Acropora*

The abundance of *Acropora* recruits was approximately 5 times higher in 2015 compared to 2016 (Figure 13). The abundance of *Acropora* recruits was similar on uninhabited island reefs (median 4.8 %, IQR 4.2 % – 7.2 %), resort island reefs (median 6.0 %, IQR 4.0 % – 11.6 %), and community island reefs (median 4.0 %, IQR 2.0 % – 6.0 %) in 2016. The abundance of *Acropora* recruits did not differ between management regimes in 2016 and had declined on uninhabited reefs (median 0.8 %, IQR 0.4 % – 2.0 %), resort reefs (median 1.2 %, IQR 0.4 % – 2.1 %) and community reefs (median 0.4 %, IQR 0.2 % – 1.6 %). The abundance of *Acropora* recruits remained very low in 2019 on uninhabited reefs (median 0.8 %, IQR 0.4 % – 1.4 %), resort reefs (median 0.8 %, IQR 0.8 % – 2.0 %) and community reefs (median 0.8 %, IQR 0.4 % – 2.0 %).

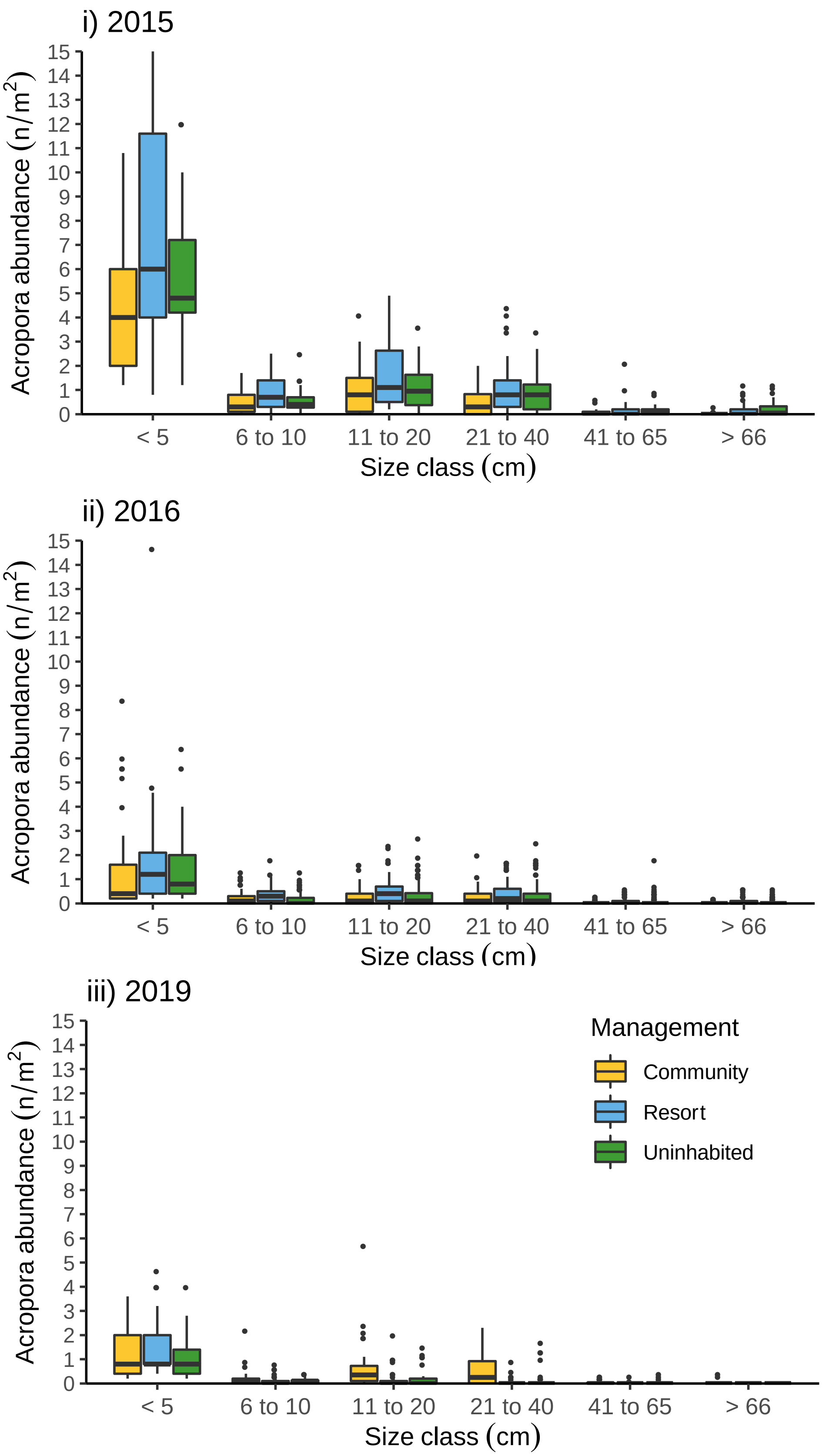


Figure 13. Size class distribution of Acropora colonies at North Ari Atoll in i) 2015, i) 2016 and iii) 2019. Data is separated by island management regime, and six size classes. The observations are the number of corals per square metre (n/m^2).

3.3.2.4. Size class frequencies distributions of Acropora

The size class frequency data of 2015, 2016 and 2019 shows a higher abundance of recruits (< 5 cm), approximately five times the abundance of larger colonies (Figure 13). The abundance of larger size classes decreases progressively. The shape of size class distributions are similar in each survey and reflect the expected exponential decline in abundance with greater size, although the abundance of corals declines for all size classes.

The baseline surveys from 2015 indicate the abundance of *Acropora* recruits (< 5cm) was higher at the resort island reefs than at community island reefs, with intermediate recruit abundance at the uninhabited island reefs. *Acropora* colonies in size classes 6 to 10 cm and 11 to 20 cm, were also more abundant at resort reefs in 2015. Most of the *Acropora* colonies observed in 2015, 2016 or 2019 were smaller than 40cm, possibly the maximum size reached since earlier disturbances (e.g. 1998 bleaching).

The decline in the abundance of *Acropora* recruits relative to 2015 was larger than declines seen for larger corals in 2016 and 2019. The abundance of recruits in 2016 was approximately one fifth of the abundance observed for all management regimes in 2015. The abundance of colonies in larger size classes was also lower after 2015. The abundance of *Acropora* in the size classes 6 to 10cm, 11 to 20cm and 21 to 40 cm also declined in 2016 relative to 2015 and remained lower than 2015 in 2019. The abundance of *Acropora* colonies larger than 41 cm was low in all surveys.

3.3.3. Porites

3.3.3.1. Percent cover and change in percent cover of *Porites*

The total percentage of the available substrate (calibrated to exclude sand) covered by the coral genus *Porites* did not differ significantly over the three survey years (χ^2(df =2) = 4.3, p > 0.05). *Porites* cover was marginally higher in 2016 than in either 2015 or 2019, though this was not significant. The highest median cover of *Porites* was recorded at Madivaru in 2016 (median 10.0 %, IQR 7.4 % – 14.0 %).

The cover of *Porites* on available substrate had approximately tripled in 2016 at two of the community island reefs, Feridhoo and Maalhos, relative to 2015 cover. *Porites* cover of available substrate remained higher in 2019 relative to 2015 at only Feridhoo (Figure 14, Table 12). In 2019, the cover of *Porites* on available substrate had declined at three resort island reefs Kan'dholhudhoo, Maayafushi and Velidhoo relative to cover in 2015. The cover of *Porites* on available substrate approximately doubled between 2015 and 2016 at two uninhabited island reefs, Madivaru and Vihamaafaru. Though the cover was lower in 2019, *Porites* continued to occupy more of the available substrate relative to 2015 at Madivaru and Vihamaafaru.

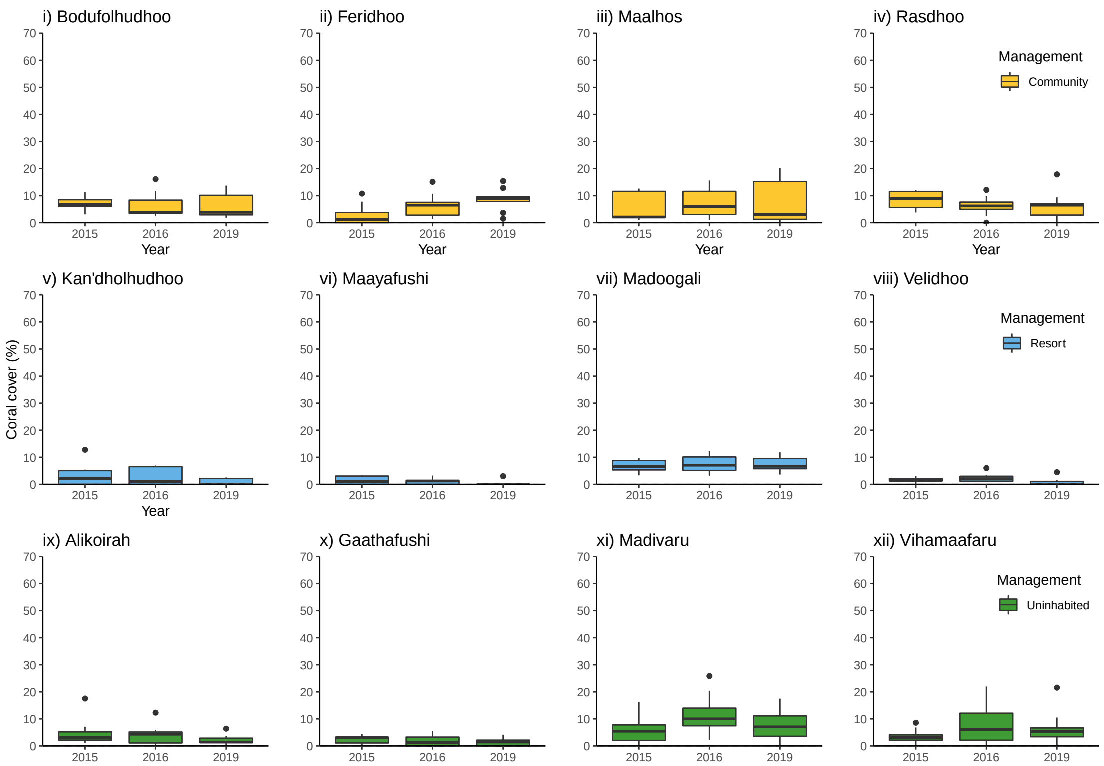


Figure 14. The percent cover of the coral genus Porites at each island surveyed in North Ari Atoll in 2015, 2016 and 2019. Islands are ordered from left to right according to management regimes of uninhabited islands, resort islands and community islands. COTS are known to have been present at in 2015 at Alikoirah, Gaathafushi and Maayafushi, whilst also at Kan'dholhudhoo in 2016. Data is calibrated for available substrate by removing sand.

Table 12. Median percent cover and interquartile range (IQR) of *Porites* observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	6.7	6, 8.5	3.8	3.5, 8.3	3.8	2.9, 10.1
	Feridhoo	1.2	0.0, 3.8	6.5	2.8, 7.5	8.9	7.8, 9.5
	Maalhos	2.1	2, 11.6	6	3, 11.6	3.1	1.3, 15.2
	Rasdhoo	8.9	5.6, 11.5	6.2	4.9, 7.6	6.5	2.8, 7.1
Resort	Kan'dholhudhoo	2.1	0.0, 5.1	1.1	0.0, 6.5	0.0	0.0, 2.2
	Maayafushi	1.1	0.0, 3.1	1.2	0.0, 1.4	0.0	0.0, 0.0
	Madoogali	6.5	5.3, 8.8	7.1	5.2, 10.1	6.7	5.8, 9.5
	Velidhoo	1.4	1.3, 2.1	2.1	1.2, 3	0.0	0.0, 1.1
Uninhabited	Alikoirah	3.1	2.2, 5.2	4.3	1.1, 5.2	1.4	1.3, 2.9
	Gaathafushi	3.1	1.1, 3.2	1.3	0.0, 3.3	1.5	0.0, 2.2
	Madivaru	5.4	2.1, 7.8	10.0	7.4, 14	7	3.6, 11.1
	Vihamaafaru	3.2	2.1, 4.1	6	2.1, 12.1	5.3	3.4, 6.7

3.3.3.2. Habitat distribution patterns of *Porites*

The percentage of the available substrate (calibrated to exclude sand) covered by the coral genus *Porites* in 2015 was generally higher at community island reefs than at uninhabited island reefs and resort island reefs (Figure 15), and the impacts of management was altered significantly local exposure conditions ($\chi 2(df = 2) = 17.77$, $p < 0.05$) and marginally by island location ($\chi 2(df = 2) = 5.78$, $p = 0.05$). The baseline surveys undertaken in 2015 suggest that *Porites* colonies occupy more of the available substrate on outer island reefs than on inner island reefs, and also on locally exposed reefs than on sheltered reefs.

The highest cover of *Porites* observed for individual transects was at uninhabited island reefs (17.5 %). The differences in cover of *Porites* in 2016 between management regimes were less apparent. *Porites* cover remained higher at community island reefs (median 5.7 %, IQR 3.0 % – 8.7 %) when compared to resort island reefs (median 2.1 %, IQR 1.05 % – 6.13 %), but did not differ to uninhabited island reefs (median 4.8 %, IQR 1.39 % – 10.25 %). The highest observations of *Porites* cover were again at uninhabited reefs (25.84 %).

In 2019, the *Porites* continued to occupy more of the available substrate at community island reefs (median 6.2 %, IQR 2.61 % – 9.67 %) than at uninhabited island reefs (median 2.7 %, IQR 1.41 % – 5.94 %) and resort island reefs (median 0.0 %, IQR 0.0 % – 3.64 %) where *Porites* cover had dropped to very low levels.

Disturbance from the bleaching event in 2016, and resulting impacts on colonies of *Porites*, may have varied in its extent according to habitat. Greater declines in the cover of *Porites* may have occurred at inner islands relative to outer islands. The historical presence of COTS did not influence the percent cover of *Porites* (χ^2(df =2) = 0.80, $p > 0.05$)

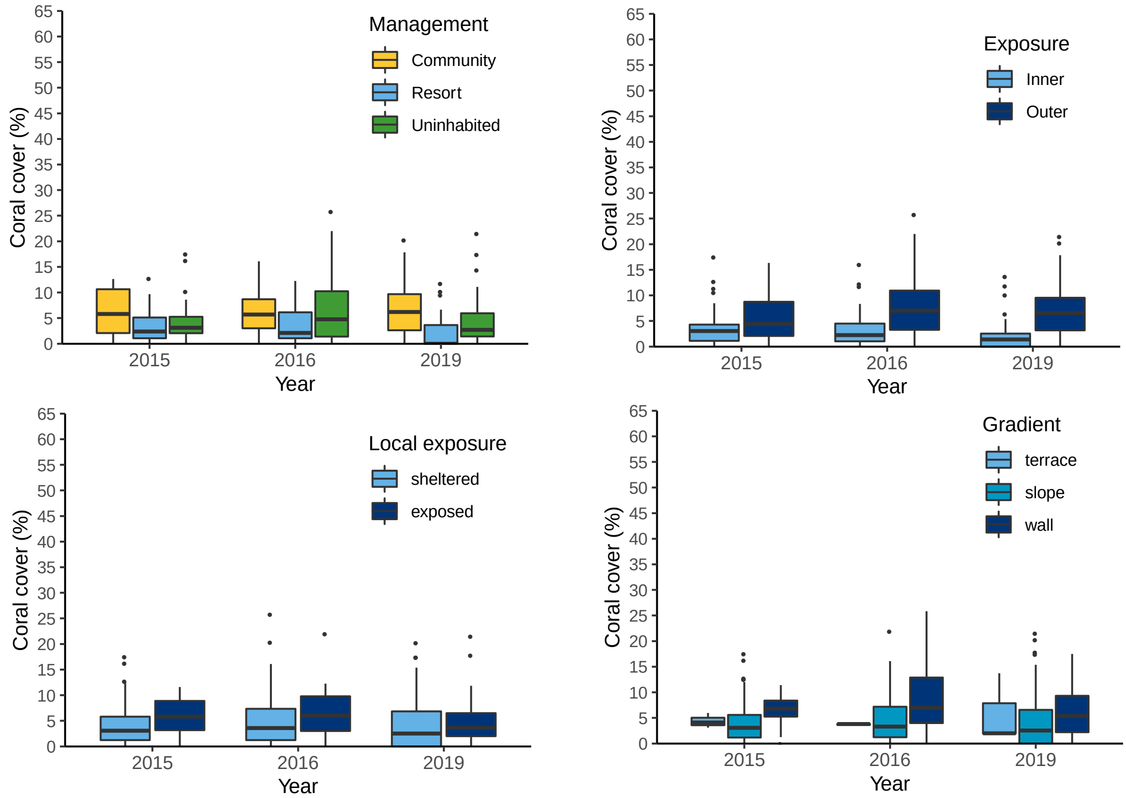


Figure 15. Percent cover of the coral genus Porites at North Ari Atoll. Data was collected with point intercept transects and does not include recruits. Data is combined for i) management regimes of Uninhabited, Resort and Community islands, ii) Island Exposure at the Inner or Outer edge of the atoll, iii) Local exposure of the reef sites to sheltered or exposed conditions (e.g. waves, wind) and iv) The gradient of the reef of terrace, slope or wall habitat.

3.3.3.3. Recruitment patterns of *Porites*

The abundance of *Porites* recruits was highest in 2015 where all management regimes has a median number of recruits greater than 2/ m^2 (Figure 16, Table A 4). This number dropped by approximately 2-3 times by 2016, where abundance of *Porites* recruits at all management regimes was less than median 0.5/ m^2. The number of recruits increased slightly in 2019 but remained at or below a median of 1/ m^2. Recruit abundance did not differ notably between management regimes within years.

3.3.3.4. Size class frequencies distributions of *Porites*

The size class frequency data of 2015, 2016 and 2019 shows *Porites* recruits (< 5 cm), were approximately 3 times more abundant than larger colonies (Figure 16). The abundance of larger size classes decreased progressively, and the shape of the size class distribution is similar in each survey year, reflecting the expected exponential decline in abundance with greater size. The largest declines observed between years were for recruits, although in 2019 the abundance of all size classes is lower than previous years. Colonies larger than 40 cm were rare in all of the survey years.

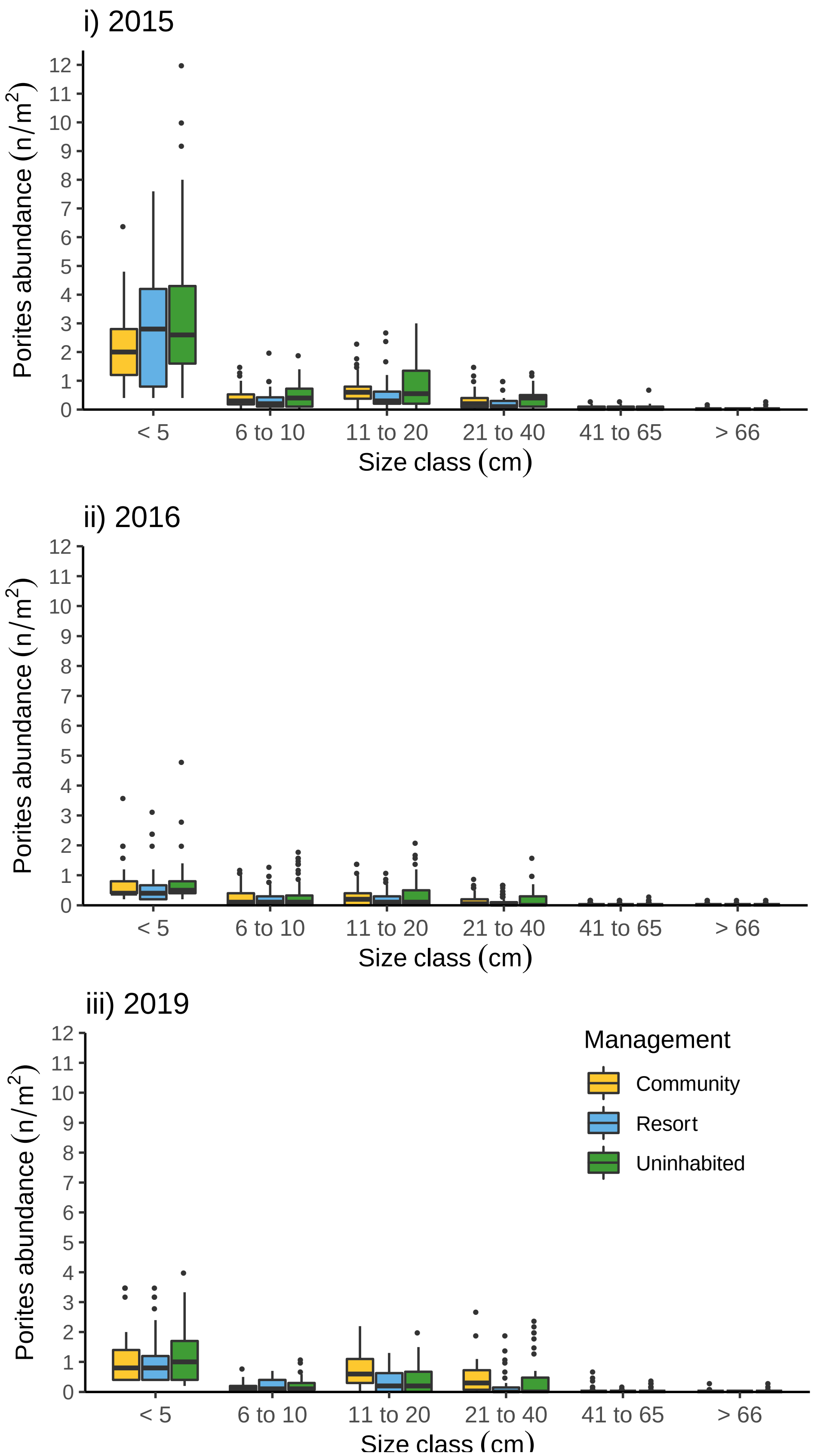


Figure 16. Size class distribution of *Porites* colonies at North Ari Atoll in i) 2015, i) 2016 and iii) 2019. The data is separated by island management regime, and six size classes. The observations are the number of corals per square metre (n/m^2).

3.3.4. *Pocillopora*

3.3.4.1. Percent cover and change in percent cover of *Pocillopora*

The percent cover of *Pocillopora* did not vary significantly between years (χ^2(df =2) = 1.21, p > 0.05). *Pocillopora* rarely occupied more than 5 % of the available substrate in any of the survey years. *Pocillopora* were not observed at Alikoirah, Gaathafushi or Maayafushi after COTS were observed at each of these islands (Figure 17). There are no other noticeable changes in the cover of *Pocillopora* on available substrate in 2019 relative to 2016 other than for the resort island Velidhoo (Table 13). In 2019, the cover of *Pocillopora* on available substrate was relatively high at the reefs of uninhabited Vihamaafaru (median 2.7 %, IQR 0.0 % – 4.35 %) and at the reefs of the resort island Madoogali (median 2.7 %, IQR 0.0 % – 4.35 %) which was previously degraded.

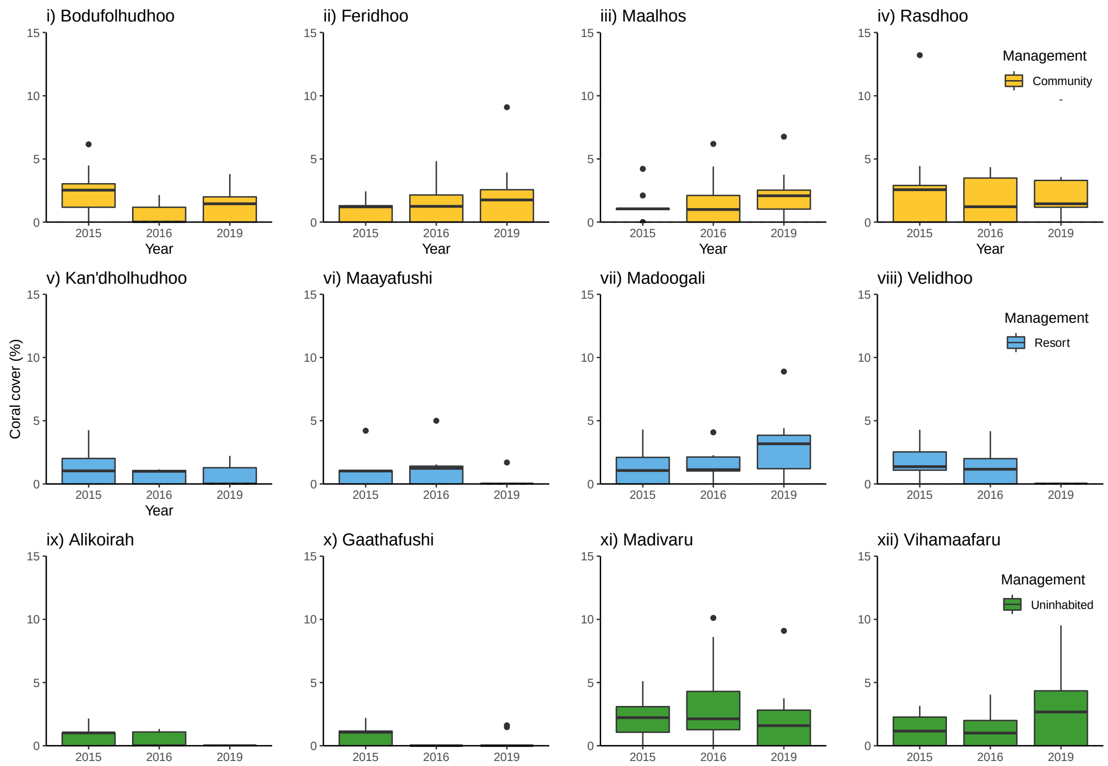


Figure 17.The percent cover of the coral genus *Pocillopora* at each island surveyed in North Ari Atoll in 2015, 2016 and 2019. Islands are ordered from left to right according to management regimes of uninhabited islands, resort islands and community islands. COTS are known to have been present at in 2015 at Alikoirah, Gaathafushi and Maayafushi, whilst also at Kan'dholhudhoo in 2016. Data is calibrated for available substrate by removing sand.

Table 13. Median percent cover and interquartile range (IQR) of *Pocillopora* observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	2.5	1.2, 3.0	0.0	0.0, 1.2	1.4	0.0, 2.0
	Feridhoo	1.2	0.0, 1.3	1.3	0.0, 2.2	1.8	0.0, 2.6
	Maalhos	1.1	1.0, 1.1	1.0	0.0, 2.1	2.1	1.0, 2.5
	Rasdhoo	2.6	0.0, 2.9	1.2	0.0, 3.5	1.4	1.2, 3.3
Resort	Kan'dholhudhoo	1.0	0.0, 2.0	1.0	0.0, 1.1	0.0	0.0, 1.3
	Maayafushi	1.0	0.0, 1.1	1.2	0.0, 1.4	0.0	0.0, 0.0
	Madoogali	1.1	0.0, 2.1	1.1	1.0, 2.1	3.2	1.2, 3.8
	Velidhoo	1.4	1.1, 2.5	1.2	0.0, 2.0	0.0	0.0, 0.0
Uninhabited	Alikoirah	1.0	0.0, 1.0	0.0	0.0, 1.1	0.0	0.0, 0.0
	Gaathafushi	1.1	0.0, 1.2	0.0	0.0, 0.0	0.0	0.0, 0.0
	Madivaru	2.2	1.1, 3.1	2.1	1.3, 4.3	1.6	0.0, 2.8
	Vihamaafaru	1.2	0.0, 2.3	1.0	0.0, 2.0	2.7	0.0, 4.3

3.3.4.2. Habitat distribution patterns of *Pocillopora*

The percentage of the available substrate (calibrated to exclude sand) covered by the coral genus *Pocillopora* in 2015 was generally below 5 % and similar for all management regimes (Figure 18). The highest cover of Pocillopora observed was for a transect at a community island reef (13.2 %). No differences were observed between management regimes in the percentage of available substrate occupied by Pocillopora in 2015. In 2016 less of the available substrate was occupied by *Pocillopora* at uninhabited island reefs (median 0.0 %, IQR 0.0 % – 1.56 %), than at either community (median 1.1 %, IQR 0.0 % – 2.15 %) or resort island reefs (median 1.1 %, IQR 0.0 % – 1.44 %). Observations made in 2019 suggest more of the available substrate was occupied by Pocillopora at community island reefs (median 1.5 %, IQR 0.0 % – 2.75 %) than at either resort (median 0.0 %, IQR 0.0 % – 1.25 %) or uninhabited island reefs (median 0.0 %, IQR 0.0 % – 1.89 %).

There was an interaction in the analytical model between management and island location and local island exposure which shows that management impacts *Pocillopora* cover differently under different environmental conditions. The percent cover of *Pocillopora* was significantly higher on inner atoll resort island reefs than on outer atoll reefs of community islands ($df = 300.78$, $t = 2.13$, $p < 0.05$) or uninhabited islands ($df = 79.44$, $t = 2.02$, $p < 0.05$), despite outer atoll reefs having significantly higher cover of *Pocillopora* when all data is combined ($\chi^2(df = 1) = 13.22$, $p < 0.001$).

The baseline surveys undertaken in 2015 suggest that *Pocillopora* colonies occupied similar amounts of the available substrate on inner and outer islands (Figure 18ii). However, the cover of *Pocillopora* subsequently declined on inner island reefs where *Pocillopora* was rarely observed in 2019. *Pocillopora* colonies also occupied similar amounts of the available substrate on locally sheltered and exposed reefs in 2015 and 2016, however in 2019 *Pocillopora* colonies occupied more of the available substrate on locally exposed reefs. In 2015, *Pocillopora* colonies occupied more of the available substrate on upward facing terrace reefs than other slope or wall habitats, however in 2016 and 2019 cover of *Pocillopora* was greater in wall habitats than either slope or terrace habitats. Historical presence of COTS did not significantly influence the cover of *Pocillopora* ($\chi^2(df = 1) = 0.17$, $p > 0.05$).

3.3.4.3. Recruitment patterns of *Pocillopora*

The abundance of *Pocillopora* recruits was approximately greater than median 2.0 recruits/ m^2 at all management regimes in 2015, with the highest recruit abundance at community island reefs (median 3.2, IQR 2.4, 5.0) (Figure 19, Table 13). In 2016, the abundance of *Pocillopora* recruits had declined to less than a median of 0.5 recruits/ m^2 across management regimes. The abundance of *Pocillopora* recruits in 2019 remained in lower than 2015 levels but increased slightly from 2016 to a median greater than 1.2/ m^2 for all management regimes.

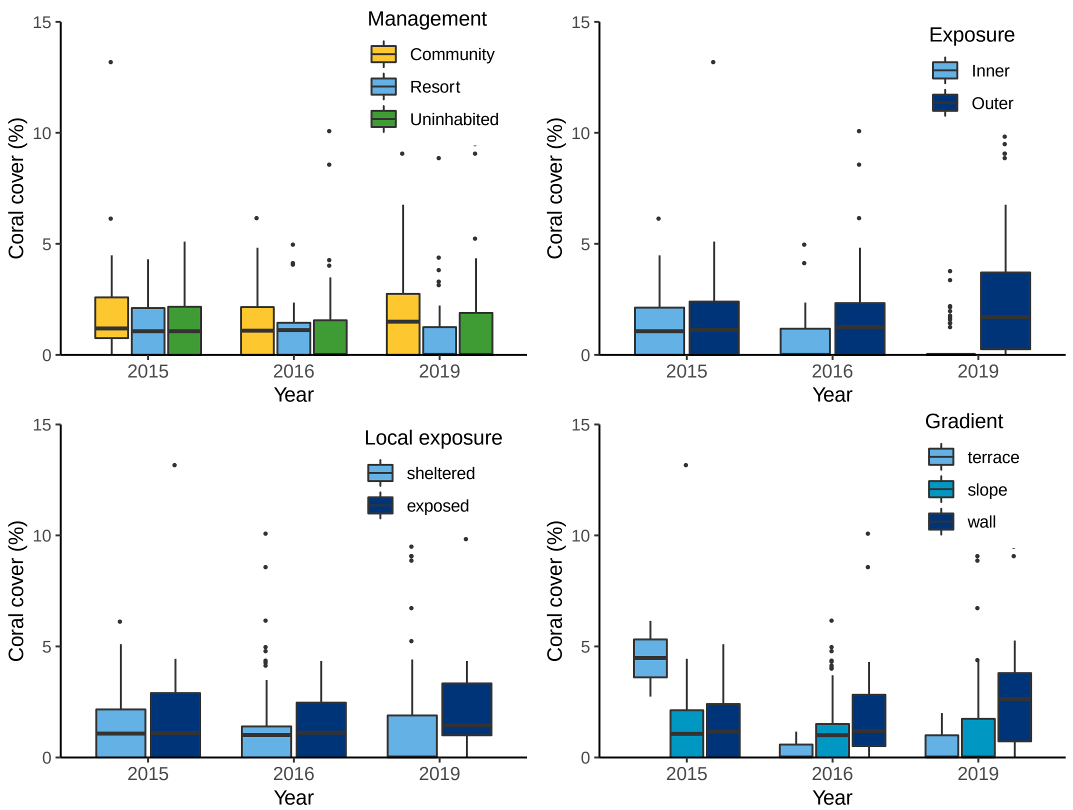


Figure 18. Percent cover of the coral genus *Pocillopora* at North Ari Atoll. Data was collected with point intercept transects and does not include recruits. Data is combined for i) management regimes of Uninhabited, Resort and Community islands, ii) Island Exposure at the Inner or Outer edge of the atoll, iii) Local exposure of the reef sites to sheltered or exposed conditions (e.g. waves, wind) and iv) The gradient of the reef of terrace, slope or wall habitat.

The abundance of *Pocillopora* recruits remained in 2019 for uninhabited island reefs (median 1.2 per m^2, IQR 0.8 – 1.2 per m^2), resort island reefs (median 1.2 per m^2, IQR 0.4 – 1.2 per m^2) and community island reefs (median 1.4 per m^2, IQR 0.4 – 1.4 per m^2).

3.3.4.4. Size class frequencies distributions of *Pocillopora*

The size class frequency data shows the abundance of *Pocillopora* recruits (< 5 cm), described above, was considerably greater than the abundance of larger colonies for all years. Colonies of *Pocillopora* larger than 5 cm in diameter were rare in either across all years and management regimes

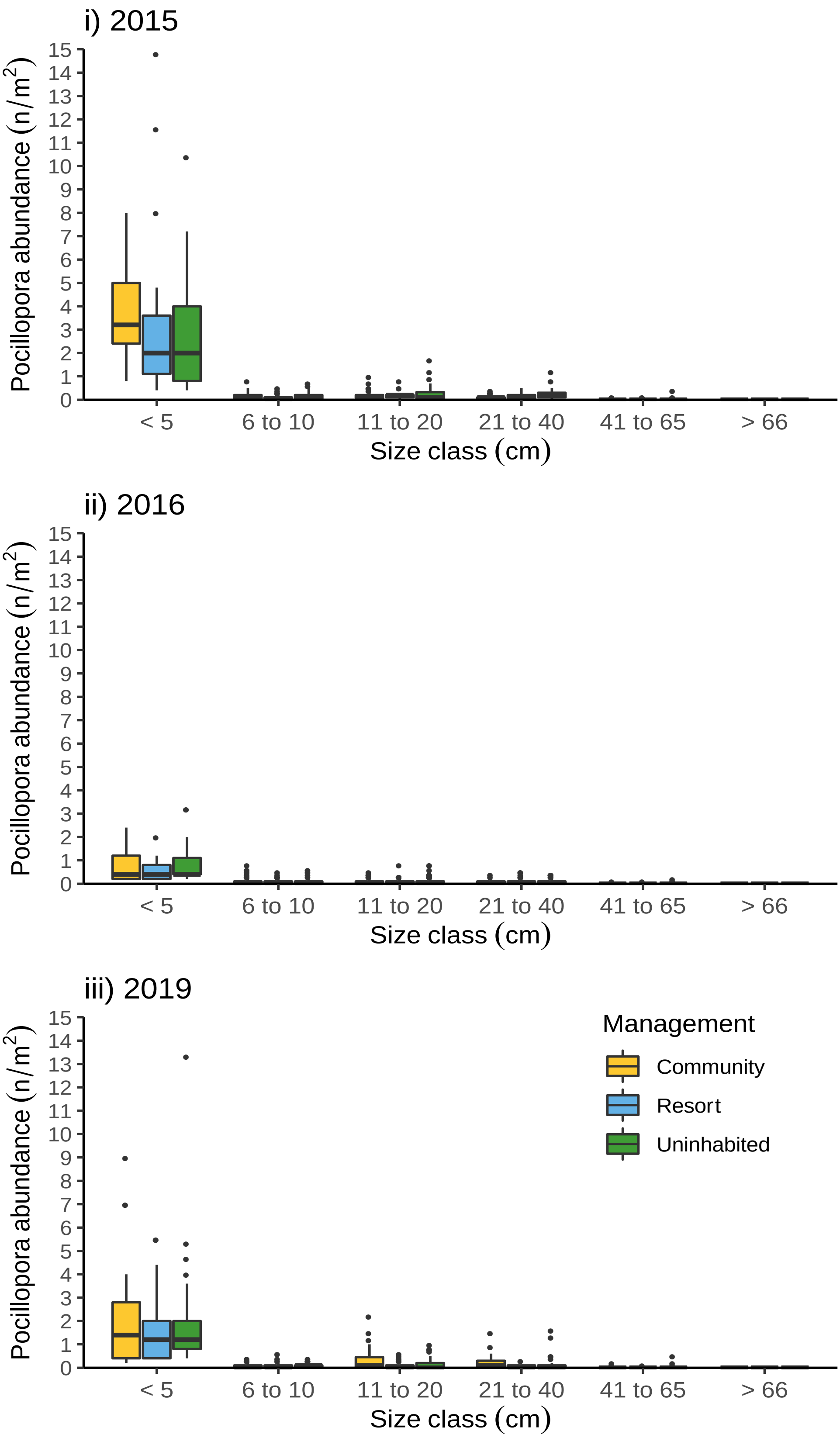


Figure 19. Size class distribution of *Pocillopora* colonies at North Ari Atoll in i) 2015, i) 2016 and iii) 2019. The data is separated by island management regime, and six size classes. The observations are the number of corals per square metre (n/m^2).

3.3.5. *Pavona*

3.3.5.1. Percent cover and change in percent cover of *Pavona*

he percent cover of *Pavona* was similar between 2015 and 2016 but declined significantly in 2019 (χ^2(df =2) = 13.37, $p < 0.01$). *Pavona* were only observed at a single transect at Gaathafushi after COTS were observed in 2016. *Pavona* generally occupied very little of the available substrate in North Ari Atoll (Figure 20) with the exception of reefs at the uninhabited inland of Madivaru (Table 14).

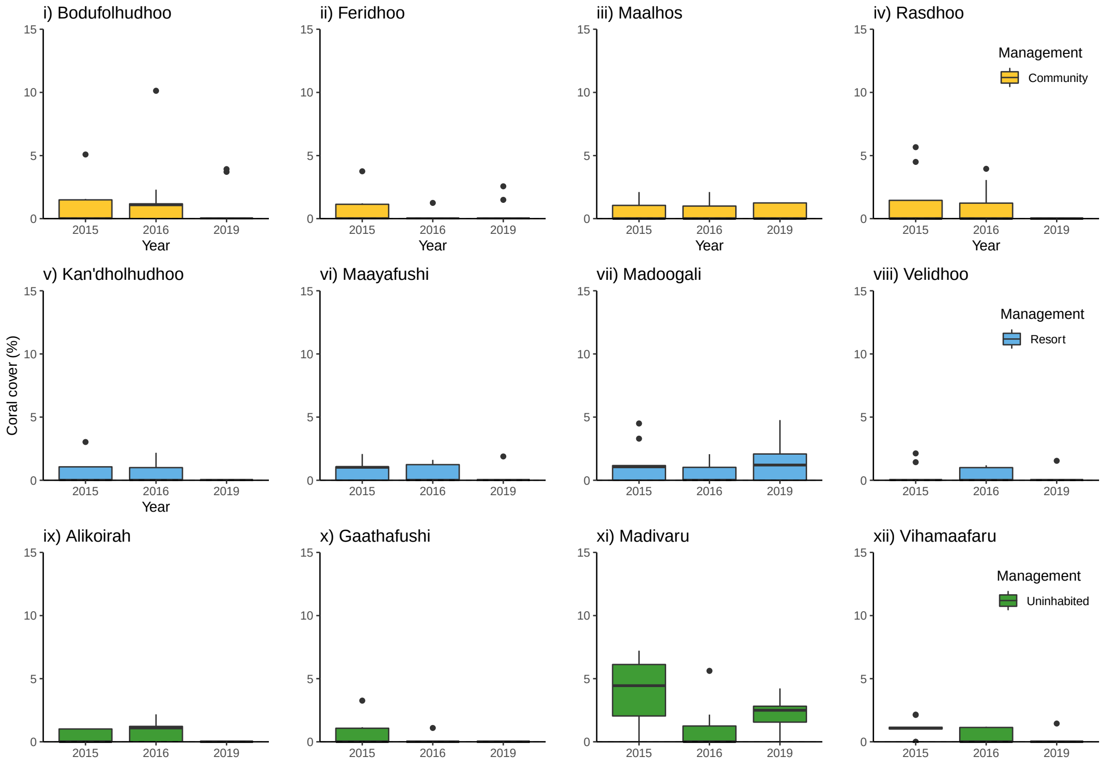


Figure 20. The percent cover of the coral genus *Pavona* at each island surveyed in North Ari Atoll in 2015, 2016 and 2019. Islands are ordered from left to right according to management regimes of uninhabited islands, resort islands and community islands. COTS are known to have been present at in 2015 at Alikoirah, Gaathafushi and Maayafushi, whilst also at Kan'dholhudhoo in 2016. Data is calibrated for available substrate by removing sand.

Table 14. Median percent cover and interquartile range (IQR) of *Pavona* observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	0.0	0.0, 1.5	1.1	0.0, 1.2	0.0	0.0, 0.0
	Feridhoo	0.0	0.0, 1.1	0.0	0.0, 0.0	0.0	0.0, 0.0
	Maalhos	0.0	0.0, 1.1	0.0	0.0, 1.0	0.0	0.0, 1.3
	Rasdhoo	0.0	0.0, 1.4	0.0	0.0, 1.2	0.0	0.0, 0.0
Resort	Kan'dholhudhoo	0.0	0.0, 1.1	0.0	0.0, 1.0	0.0	0.0, 0.0
	Maayafushi	1.0	0.0, 1.1	0.0	0.0, 1.2	0.0	0.0, 0.0
	Madoogali	1.1	0.0, 1.2	0.0	0.0, 1.0	1.2	0.0, 2.1
	Velidhoo	0.0	0.0, 0.0	0.0	0.0, 1.0	0.0	0.0, 0.0
Uninhabited	Alikoirah	0.0	0.0, 1.0	1.1	0.0, 1.2	0.0	0.0, 0.0
	Gaathafushi	0.0	0.0, 1.1	0.0	0.0, 0.0	0.0	0.0, 0.0
	Madivaru	4.4	2.0, 6.1	0.0	0.0, 1.3	2.5	1.6, 2.8
	Vihamaafaru	1.1	1.0, 1.1	0.0	0.0, 1.1	0.0	0.0, 0.0

3.3.5.2. Habitat distribution patterns of *Pavona*

There was no interaction in the analytical model between management either island location or local island exposure indicating no impact of management on the percent cover of *Pavona*. *Pavona* was rarely observed at all management regimes in 2015 and 2016 and were virtually absent from all management regimes in 2019. The percentage of the available substrate (calibrated to exclude sand) covered by the coral genus Pavona in 2015 was generally below 3 % although slightly higher for uninhabited island reefs, than resort or community island reefs (Figure 21). The highest cover of Pavona observed was for a transect at an uninhabited island reef (7.22 %)

The percent cover of *Pavona* differed significantly between inner and outer atoll reefs (χ^2(df =1) = 5.62, $p < 0.05$) and the baseline surveys undertaken in 2015 suggest that *Pavona* colonies occupied more of the available substrate on outer island reefs than on inner island reefs, this was also true in 2019 (Figure 21ii). There was no significant difference in *Pavona* cover between local reef exposures (χ^2(df =1) = 0.08, $p > 0.05$), though cover did differ between reef gradients (χ^2(df =2) = 15.07, $p < 0.01$). In 2015, *Pavona* colonies occupied more of the available substrate in wall habitats relative to upward facing terrace reefs or slopes. However, in 2019 cover of *Pavona* was greatest in terrace habitats.

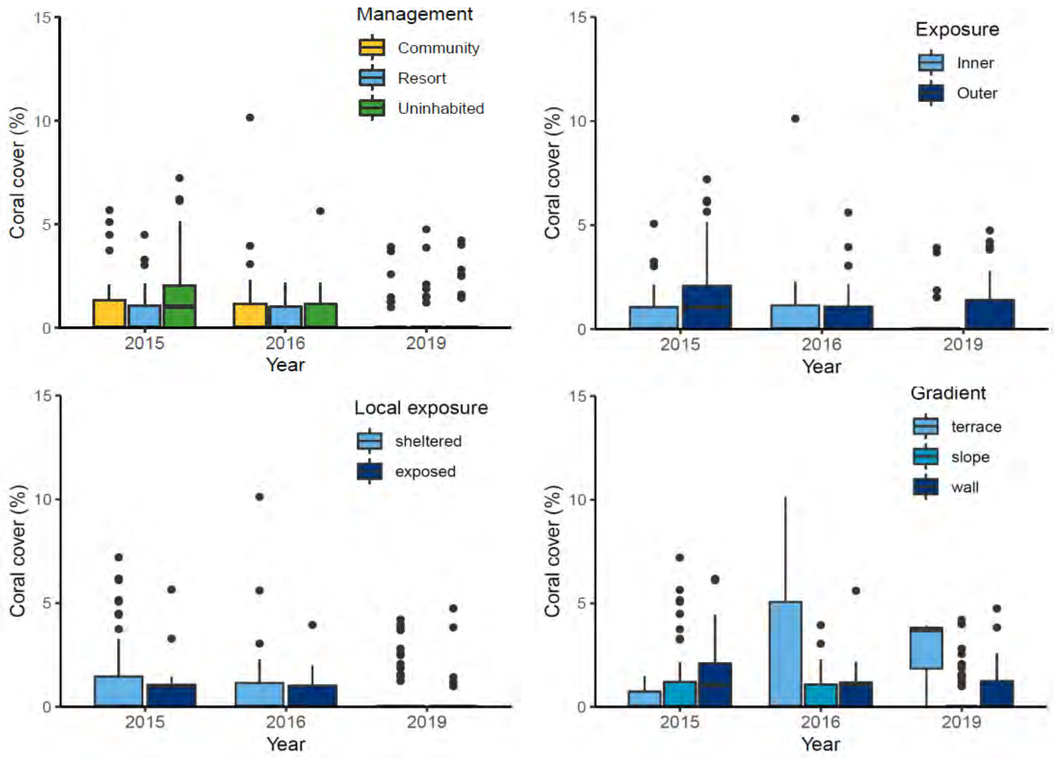


Figure 21. Percent cover of the coral genus *Pavona* at North Ari Atoll. Data was collected with point intercept transects and does not include recruits. Data is combined for i) management regimes of Uninhabited, Resort and Community islands, ii) Island Exposure at the Inner or Outer edge of the atoll, iii) Local exposure of the reef sites to sheltered or exposed conditions (e.g. waves, wind) and iv) The gradient of the reef of terrace, slope or wall habitat.

3.3.5.3. Recruitment patterns of *Pavona*

The abundance of Pavona recruits was approximately 2 times higher on uninhabited island reefs compared to resort island reefs and community island reefs in 2015 (Figure 22, Table A 6). The lowest abundance of Pavona recruits was observed during the 2016 surveys for all management regimes. In 2019, the abundance of Pavona recruits had increased on all management regimes to median greater than 5 recruits/ m^2.

3.3.5.4. Size class frequencies distributions of *Pavona*

The size class frequency data of 2015, 2016 and 2019 shows the abundance of *Pavona* recruits (< 5 cm), described above, was greater than the abundance of larger colonies for all years. In 2015, *Pavona* colonies of 6 to 10 cm and 11 to 20 cm diameter were scarce at all management regimes (Table A 6). This pattern was similar in 2016 and 2019. Colonies of *Pavona* larger than 20 cm in diameter were rare at all management regimes and years.

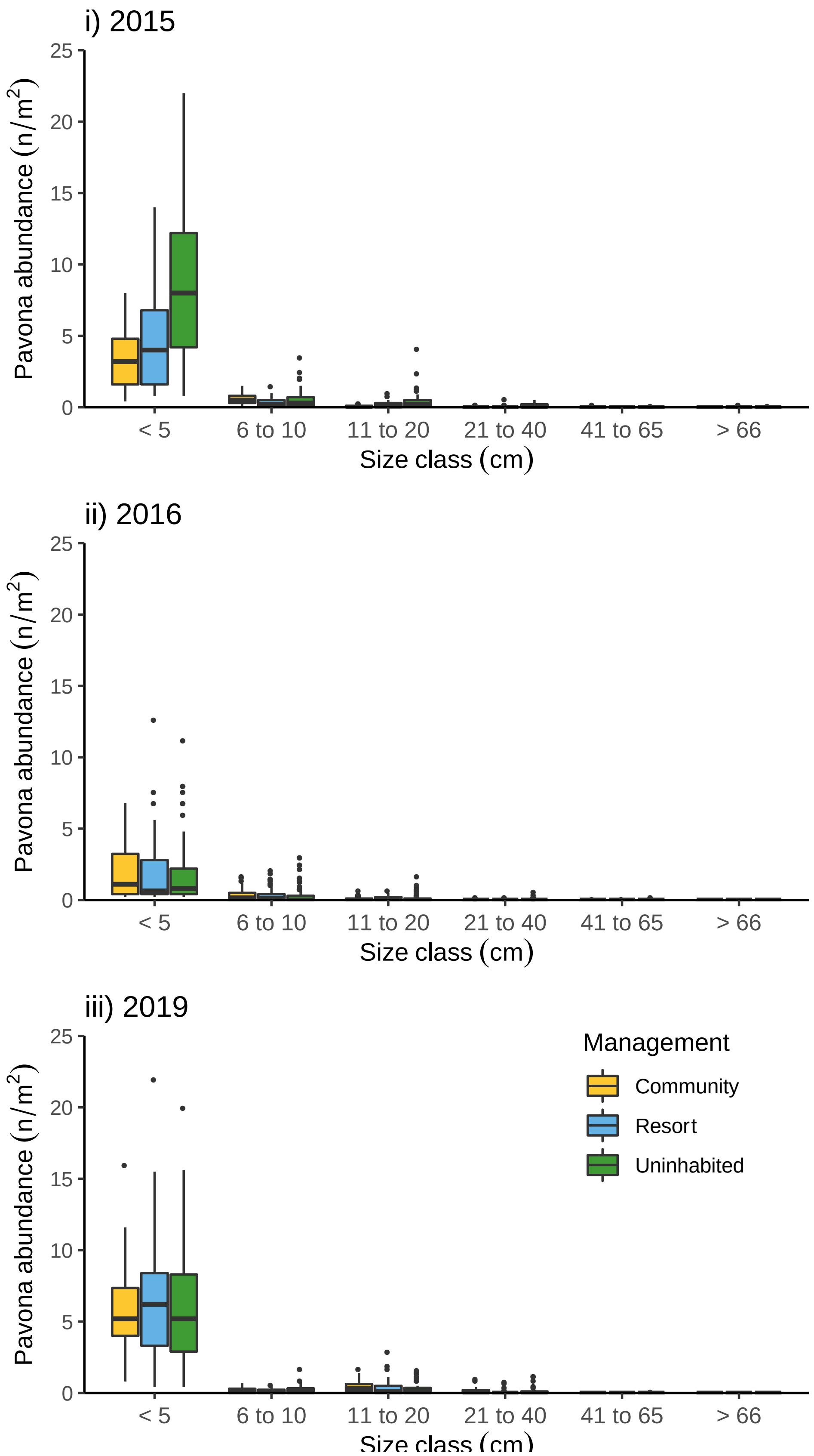


Figure 22. Size class distribution of *Pavona* colonies at North Ari Atoll in i) 2015, i) 2016 and iii) 2019. The data is separated by island management regime, and six size classes. The observations are the number of corals per square metre (n/m^2).

3.4. Impacts of coral bleaching

3.4.1. General observations

A coral bleaching event was observed to widely impact corals of North Ari Atoll in 2016 (bleached or dead colonies: median 57.7 %, IQR 35.08 % – 77.77%). No corals were observed to be bleached, or dead as a result of bleaching, in 2015 (median 0 %, IQR 0 % – 0 %). In 2019, the abundance and percent cover of corals had declined on most reefs at North Ari Atoll, and less than 1 % of the coral colonies observed were bleached or dead (median 0 %, IQR 0 % – 0 %).

There was no significant difference between management regimes of percent of all corals bleached, however there was an interaction in the analytical model between management and island location (χ^2(df =2) =8.99, $p< 0.05$) and local island exposure (χ^2(df =2) =17.03, $p < 0.01$) which indicates management impacts the proportion of colonies bleached under different environmental conditions.

The percent of dead corals was lower on outer atoll uninhabited island reefs than on inner community reefs by 20.5 % (± 9.2 %S.E., df=12.06, t=2.22, $p < 0.05$). The percent of dead corals was lower on inner atoll community island reefs than on outer atoll resort reefs by 31.0 % (± 8.3 %S.E., df=5.94, t=3.74, $p < 0.01$).

The percent of dead corals was lower on exposed community island reefs than on sheltered uninhabited island reefs by 30.7 % (± 7.08 %S.E., df=99.94, t=4.34, $p < 0.01$). The percent of dead corals was lower on sheltered resort island reefs than on exposed uninhabited island reefs by 36.2 % (± 8.00 %S.E., df=91.60, t=4.15, $p < 0.01$). The percent of dead corals was lower on sheltered community island reefs than on exposed uninhabited island reefs by 31.1 % (± 7.15 %S.E., df=97.27, t=4.35, $p < 0.01$).

A prior history of COTS had a significant influence on the percent of corals that died as a result of the bleaching event. At reefs where COTS were known to have been present the percent of dead corals was 10.5 % lower (± 4.02 %S.E., df=100.76, t=2.60, $p < 0.01$).

In 2016, all coral genera were impacted to variable extents by bleaching (Figure 23) with the exception of a small number of corals that were not identified (unknown) and colonies of the genus *Oulophyllia*. When we excluded the coral recruits, the genus *Physogyra* was the least impacted by bleaching (mean 14.3 % ± S.E. 3.64 %). Coral genera were increasingly observed to be either bleached or already dead in the following order: *Physogyra, Leptastrea*, *Goniopora, Acanthastrea*, *Coscinaraea*, *Alveopora*, *Pavona*, *Diploastrea*, *Favites*, *Ctenactis*, *Astreopora*, *Turbinaria*, *Pocillopora*, *Porites*, *Montastraea*, *Hydnophora*, *Leptoseris*, *Caulastrea*, *Pachyseris*, *Echinophyllia*, *Mycedium*, *Oxypora*, *Podabacia*, *Symphyllia*, *Lobophyllia*, *Plesiastrea*, *Acropora*, *Favia*, *Montipora*, *Cyphastrea*, *Echinopora, Platygyra*, *Galaxea*, *Psammocora*, *Goniastrea*, *Gardineroseris*, *Merulina*, *Fungia*, and *Pectinia*. All colonies of the genera *Cycloseris*, *Halomitra* and *Leptoria* were either bleached or dead. At the time of survey, which was undertaken mid bleaching event, dead colonies were observed for 26 genera (Table A 7).

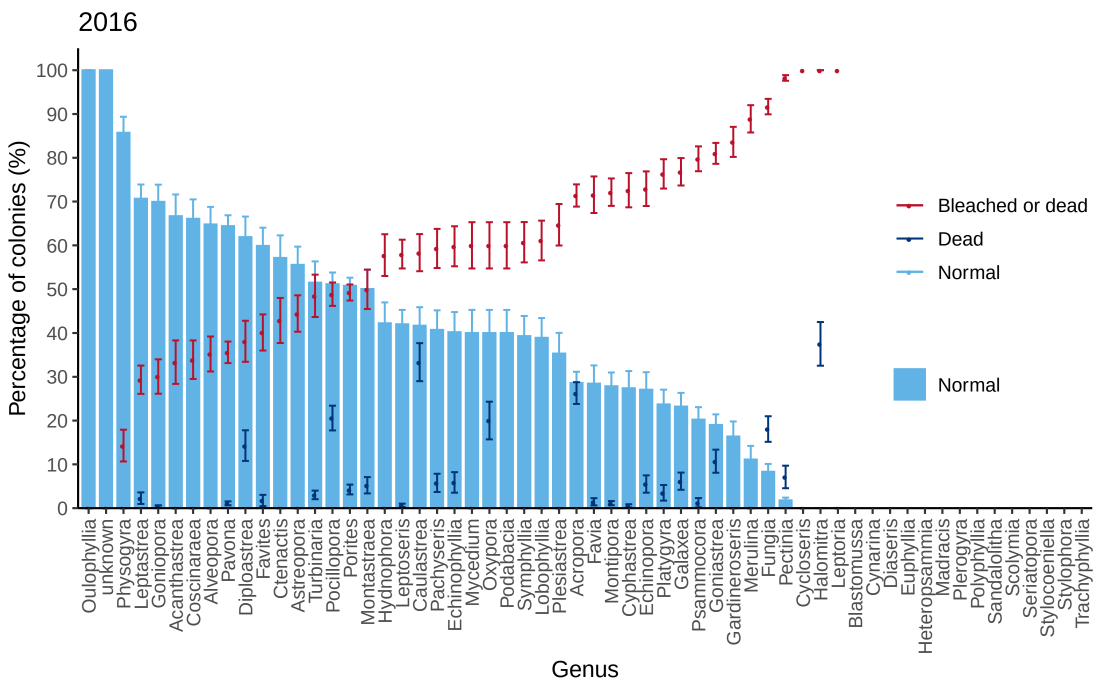


Figure 23. Percentage of coral colonies from each genus observed and larger than 5 cm in either a normal state, a bleached or dead state, or a dead state in 2016.

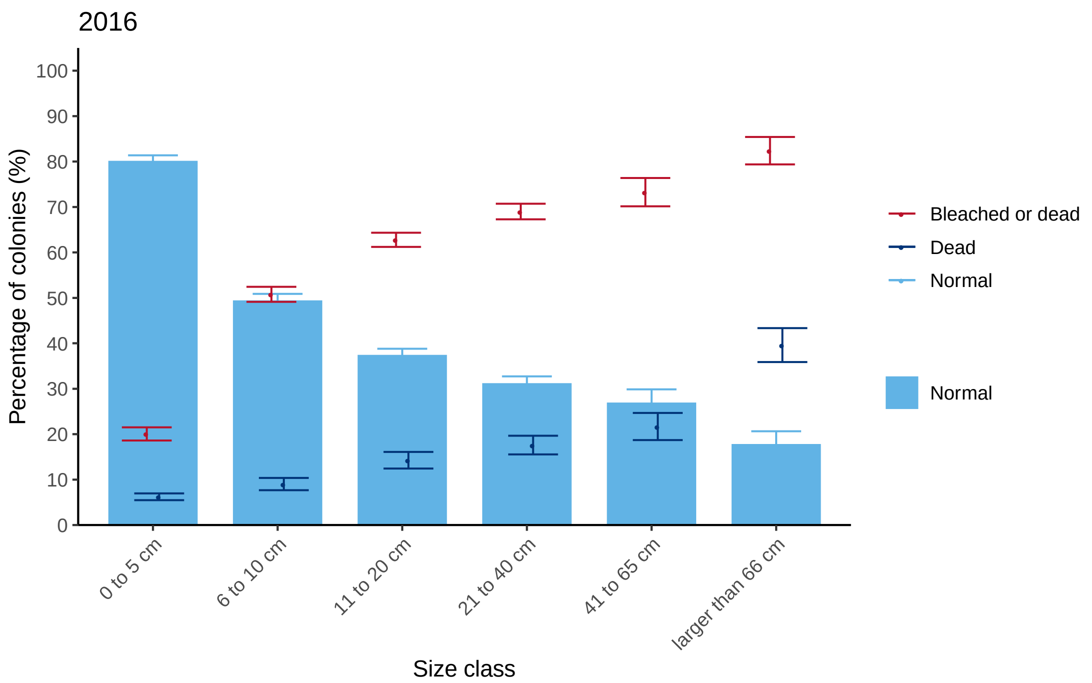


Figure 24. Percentage of coral colonies from each size class observed in either a normal state, a bleached or dead state, or a dead state in 2016.

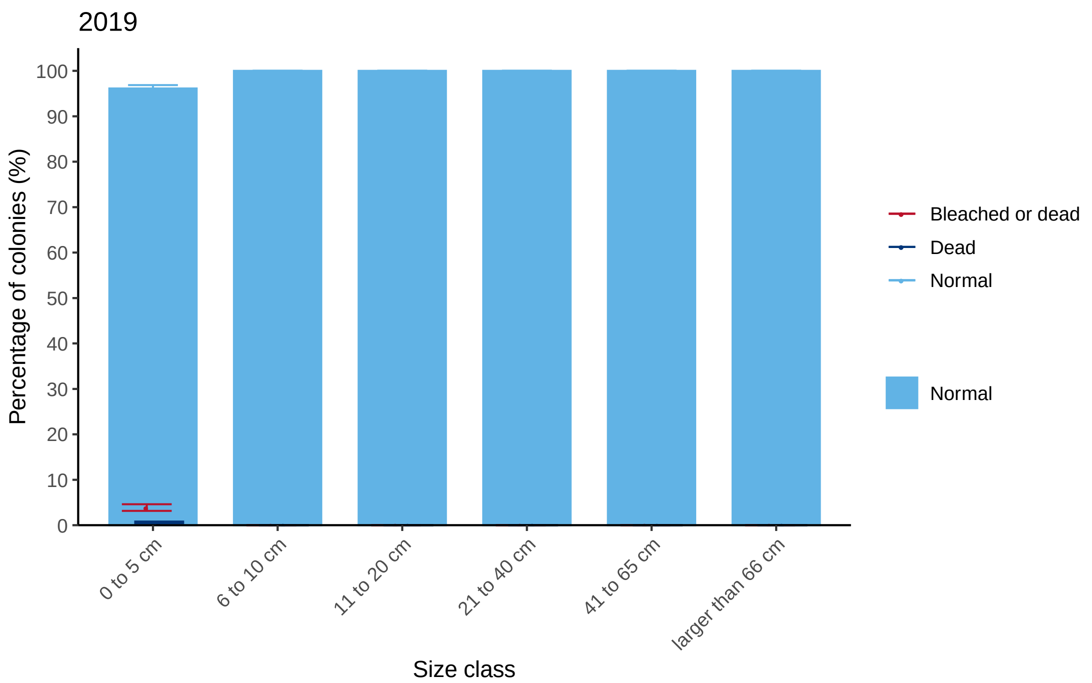


Figure 25. Percentage of coral colonies from each size class observed in either a normal state, a bleached or dead state, or a dead state in 2019.

3.4.2. Bleaching observations specific to the most abundant genera

The genera *Acropora*, *Porites*, *Pocillopora* and *Pavona* were among the coral genera with the greatest percent cover recorded in PIT surveys in 2016. These genera were also the most frequently observed in the 108 belt transects searched in surveys of the bleaching state of coral colonies in 2016.

Table 15. Percent of coral colonies of the four most common genera in each size class observed in a bleached or dead state in 2016.

Size class (cm)	*Acropora*		*Porites*		*Pocillopora*		*Pavona*	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
0 - 5	11.9	1.87	20.3	2.59	28.1	3.58	13.5	1.71
6-10	57.3	3.11	43.8	2.83	44.2	3.63	27.7	2.34
11-20	73.7	2.53	49.6	2.4	50.6	3.61	55.9	3.49
21-40	78.5	2.62	57.2	3.4	40.9	3.87	82.9	3.42
41-65	91.1	2.12	54.3	4.27	40.0	5.27	100	0.00
Larger than 66	92.1	2.26	64.1	4.18	-	-	-	-

3.4.3. *Acropora*

The genus *Acropora* was highly susceptible to bleaching in 2016, 71.4 % (± 2.54 %; 1 S.E.) of colonies were observed in a bleached or dead state (Figure 26), of these a relatively high proportion of 26.3 % (± 2.50 %; 1 S.E.) had died as a result of the bleaching at the time of survey. The state of 3188 colonies of *Acropora* was described from observations of colonies in 108 belt transects surveyed in North Ari Atoll in 2016.

The proportion of adult *Acropora* that was bleached, or dead was greater at uninhabited island reefs (median 87.0 %, IQR 50.46 % – 100.0 %) than at resort island reefs (median 72.5 %, IQR 62.27 % – 87.7 %) and was lowest on community reefs (median 60.5 %, IQR 33.33 % – 83.9 %).

The proportion of *Acropora* colonies that were bleached or dead on reefs at the outer edges of North Ari Atoll (median 64.4 %, IQR 35.0 % – 86.58 %) was lower than on inner island reefs (median 83.4 %, IQR 64.83 % – 96.35 %). The proportion of *Acropora* colonies that were bleached or dead on exposed reefs (median 62.82 %, IQR % 40.0 – 84.62 %) was lower than on sheltered reefs (median 77.8 %, IQR % 52.94 – 93.57 %). The proportion of bleached or dead corals was lower within a wall habitat (median 53.8 %, IQR % 48.8 – 69.36 %) than reefs with slope habitat (median 80.0 %, IQR % 52.94 – 93.84 %) or upward facing terrace habitat (median 81.1 %, IQR % 70.83 – 83.67 %). The proportion of bleached or dead *Acropora* increases as the size class of colonies increases (Table 15).

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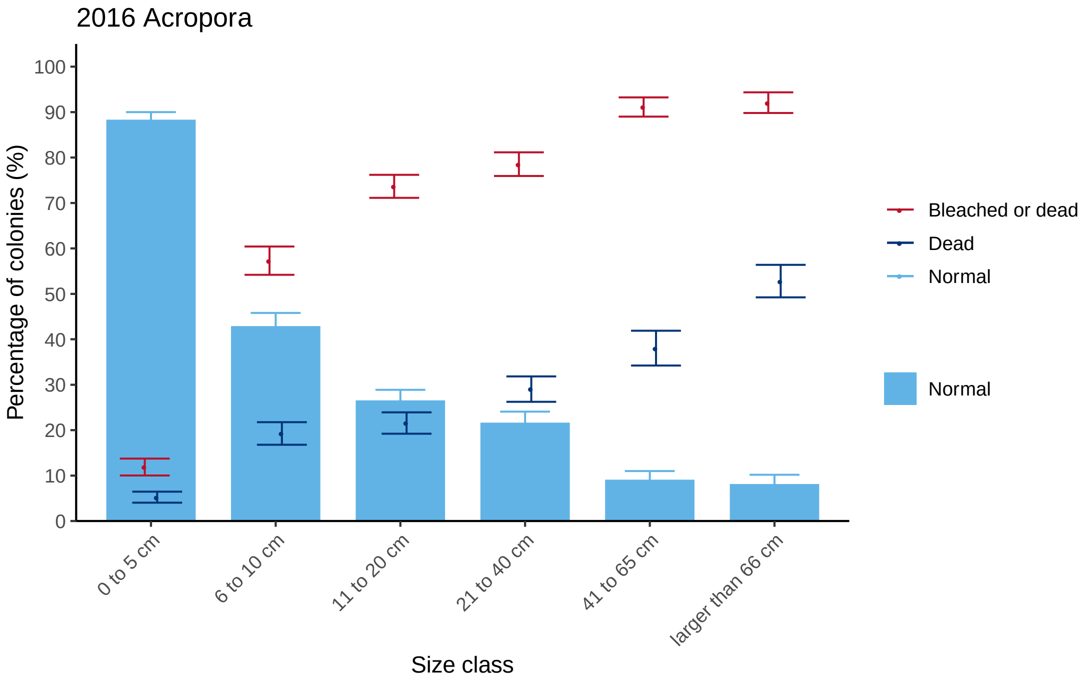


Figure 26. The percentage of *Acropora* coral colonies in each size class observed in either a normal state (light blue), a bleached or dead state (red) or dead (dark blue) in 2016.

3.4.4. *Porites*

Half of the colonies of the genus *Porites*, 49.2 % (± 1.84 %; 1 S.E.) were observed in a bleached or dead state in 2016 (Figure 27). Amongst these colonies of *Porites,* a low percentage of 4.3 % (± 1.13 %; 1 S.E.M.) had died as a result of the bleaching at the time of survey. The state of 1972 colonies of *Porites* was described from observations of colonies seen in 108 belt transects surveyed in North Ari Atoll in 2016.

The data does not suggest that the proportion of adult *Porites* that was bleached or dead differed between uninhabited island reefs (median 43.5 %, IQR 30.77 % – 56.55 %), resort island reefs (median 43.1 %, IQR 31.29 % – 65.42 %) and community island reefs (median 47.2 %, IQR 38.37 % – 64.9 %). The proportion of *Porites* colonies that were bleached or dead did not differ between reefs at the outer edges of North Ari Atoll (median 43.1 %, IQR 35.56 % – 55.21 %) and reefs inside the atoll (median 47.1 %, IQR 31.41 % – 66.67 %).

The proportion of bleached or dead *Porites* colonies was similar on sheltered (median 46.2 %, IQR 33.33 % – 62.43 %) and exposed reefs (median 43.3 %, IQR 36.36 % – 50.0 %). A greater proportion of *Porites* colonies was bleached or dead on upward facing terrace habitats (median 85.7 %, IQR 65.93 % – 92.86 %) on reef slopes (median 42.9 %, IQR 33.33 % – 60.0 %) or reef walls (median 50.0 %, IQR 33.78 % – 62.28 %).

The proportion of bleached or dead *Porites* also increases as the size class of colonies increases, however less than observed for *Acropora*. The proportion of bleached or dead *Porites* recruits was greater than the proportions observed for *Acropora* and *Pavona*, but less than for *Pocillopora*.

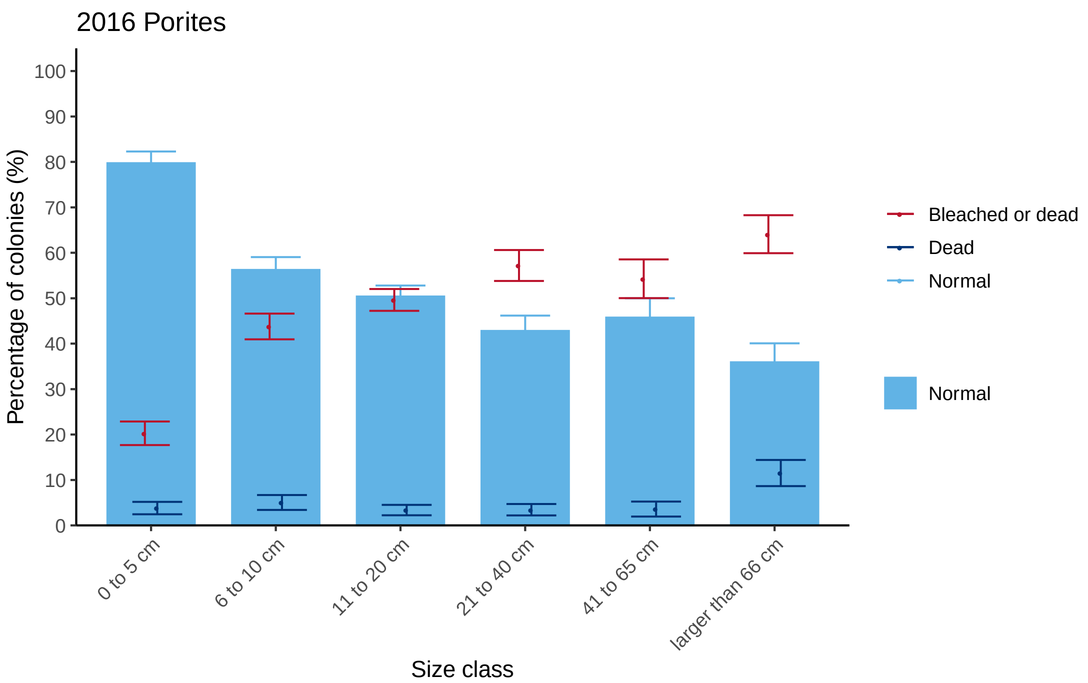


Figure 27. The percentage of *Porites* coral colonies in each size class observed in either a normal state (light blue), a bleached or dead state (red) or dead (dark blue) in 2016.

3.4.5. *Pocillopora*

Approximately half of the colonies of the genus *Pocillopora* were observed in a bleached or dead state in 2016, 48.9 % (± 2.68 %; 1 S.E.) (Figure 28). Amongst these colonies a relatively high proportion of 20.6 % (± 2.81 %; 1 S.E.) had died as a result of the bleaching at the time of survey.

There was no difference in the proportion of adult *Pocillopora* that were bleached or dead between uninhabited island reefs (median 50.0 %, IQR 32.69 % – 69.44 %), resort island reefs (median 36.9 %, IQR 20.0 % – 60.38 %) and community island reefs (median 40.0 %, IQR 25.0 % – 57.33 %). Neither did the data indicate there was a difference in the proportion of corals that bleached or died between inner island reefs (median 50.0 %, IQR 25.0 % – 66.67 %) and outer island reefs (median 38.8 %, IQR 30.0 % – 56.32 %). We also detected no difference between sheltered reefs (median 45.5 %, IQR 26.14 % – 66.67 %) and exposed reefs (median 37.5 %, IQR 25.0 % – 50.0 %). The data suggests a greater proportion of bleached corals on upward facing terrace habitats (median 66.7 %, IQR 45.83 % – 83.33 %) than on reef slopes (median 40.0 %, IQR 25.0 % – 60.0 %) and reef walls (median 50.0 %, IQR 30.3 % – 64.29 %).

The proportion of bleached or dead *Pocillopora* was lower for recruits than larger size classes but remained relatively similar for corals larger than 6 cm in diameter. The proportion of bleached or dead *Pocillopora* recruits was greater than the proportions observed for *Acropora*, *Porites* and *Pavona*.

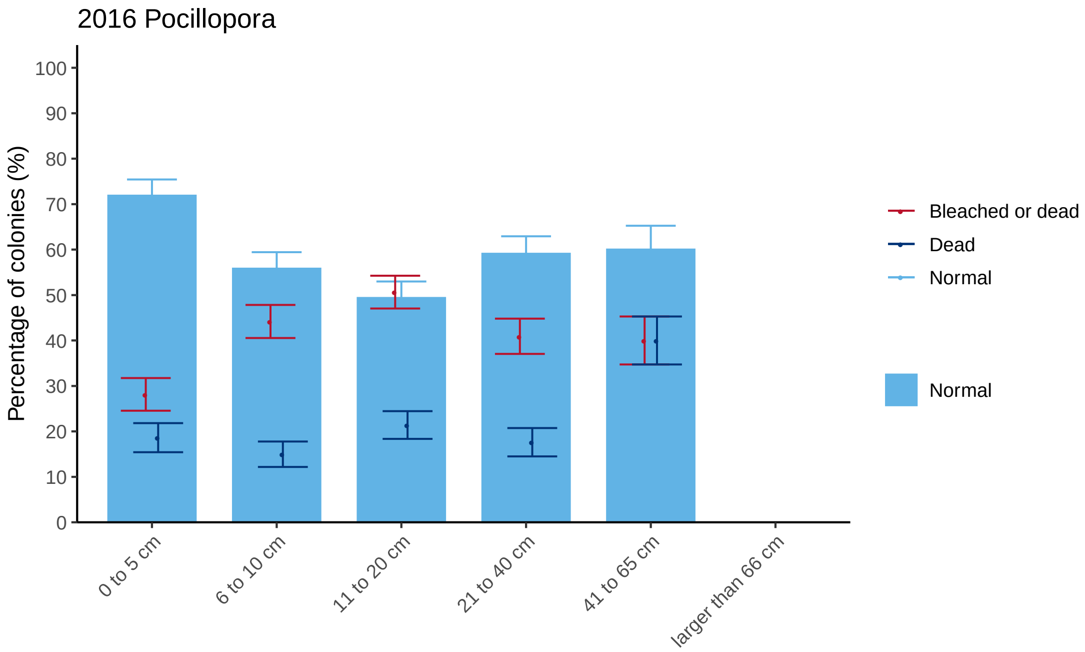


Figure 28. The percentage of *Pocillopora* coral colonies in each size class observed in either a normal state (light blue), a bleached or dead state (red) or dead (dark blue) in 2016.

3.4.6. *Pavona*

Colonies of the genus *Pavona* were amongst the least susceptible to bleaching in 2016, and 35.6 % (± 2.46 %; 1 S.E.) of colonies were observed in a bleached or dead state (Figure 29). Only a small proportion of colonies, 1.1 % (± 0.44 %; 1 S.E.M.), had died as a result of the bleaching at the time of survey. The state of 624 colonies of *Pavona* was described from observations of colonies seen in 108 belt transects surveyed in North Ari Atoll in 2016.

There were no observed differences in the proportions of bleached or dead colonies of adult *Pavona* between management regimes, island location in North Ari Atoll, local exposure or reef habitat. Proportions of dead or bleached colonies were similar on uninhabited reefs (median 27.5 %, IQR 0.0 % – 40.42 %), resort reefs (median 34.8 %, IQR 20.88 % – 53.71 %) and community reefs (median 32.1 %, IQR 5.77 % – 54.97 %). No difference was detected between inner island reefs (median 32.7 %, IQR 2.94 % – 50.0 %) and outer island reefs (median 32.1 %, IQR 12.8 % – 42.86 %). We detected no difference in the proportion of bleached or dead colonies of *Pavona* between sheltered reefs (median 33.3 %, IQR 11.76 % – 50.0 %) and exposed reefs (median 25.0 %, IQR 0.0 % – 40.0 %). There was no difference in the proportion of bleached or dead colonies of *Pavona* between upward facing terrace habitats (median 28.6 %, IQR 25.4 % – 53.57 %), slope habitats (median 33.3 %, IQR 1.92 % – 49.34 %), and wall habitats (median 30.8 %, IQR 21.34 % – 45.56 %).

The proportion of bleached or dead coral colonies increased dramatically with size of *Pavona* colonies. The proportion of bleached or dead *Pavona* recruits was lower than the proportions observed for *Pocillopora*, greater than that observed for *Acropora* and similar to observations for *Porites*.

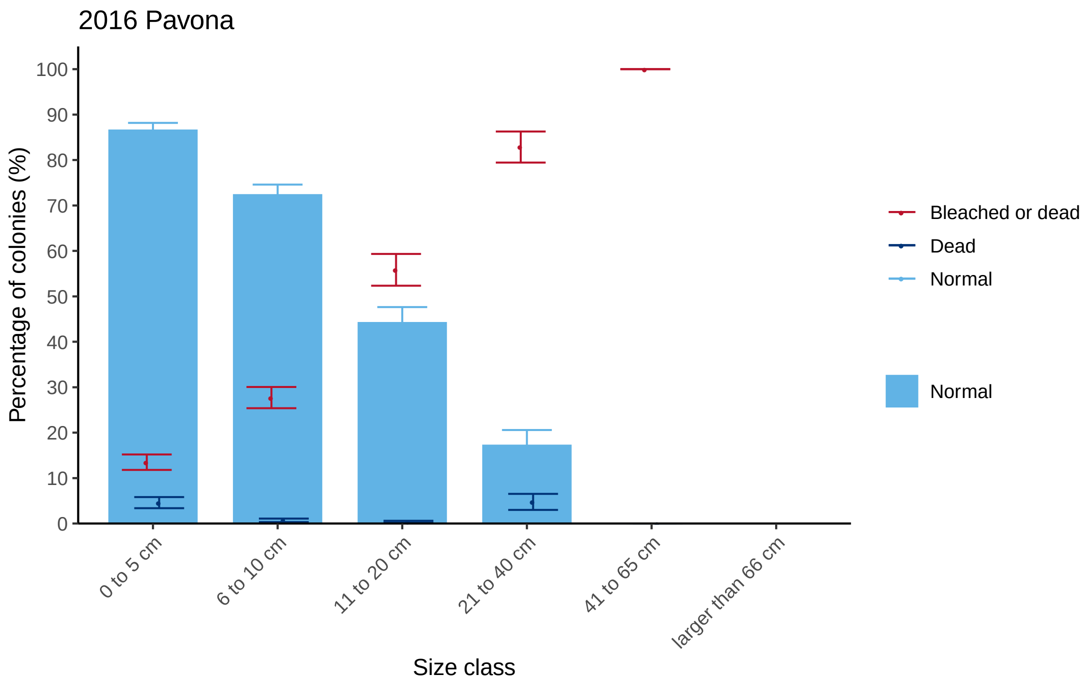


Figure 29. The percentage of *Pavona* coral colonies in each size class observed in either a normal state (light blue), a bleached or dead state (red) or dead (dark blue) in 2016.

3.5. Fish community

3.5.1. Temporal changes in the fish community

The fish community showed significant changes across the years surveyed, though different metrics responded differently (Figure 30). Fish diversity and biomass were significantly lower in 2019 (38 ± 1 spp/100 m^2 and 8.6 ± 0.6 kg/100 m^2, respectively) than in 2016 (48 ± 1 spp/100 m^2 and 24.7 ± 2.2 kg/100 m^2, respectively) and 2015 (45 ± 1 spp/100 m^2 and 29.0 ± 2.7 kg/100 m^2, respectively). Fish density was significantly higher in 2015 (796 ± 112/100 m^2), before the bleaching event, than in 2016 (418 ± 42/100 m^2) and 2019 (322 ± 31/100 m^2). Fish biomass was significantly lower in 2019 in all management regimes (8.1 ± 0.8 kg/100 m^2 on community island reefs, 8.5 ± 0.7 kg/100 m^2 on resort island reefs and 9.3 ± 1.3 kg/100 m^2 on uninhabited island reefs) (Figure 31). On uninhabited island reefs, fish biomass started to decrease significantly in 2016, whereas it did not drop significantly on community and resort island reefs until 2019. The decline in biomass occurred across all reefs and the 2019 surveys had the lowest fish biomass, without exception (Figure 32).

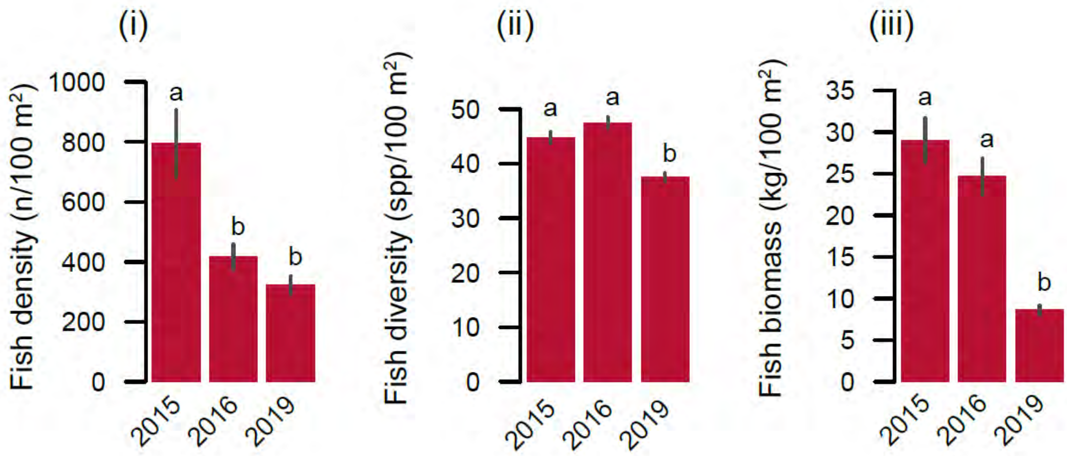


Figure 30. Mean fish density (i), diversity (ii) and biomass (iii) across the 12 islands surveyed in North Ari in 2015, 2016 and 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between years.

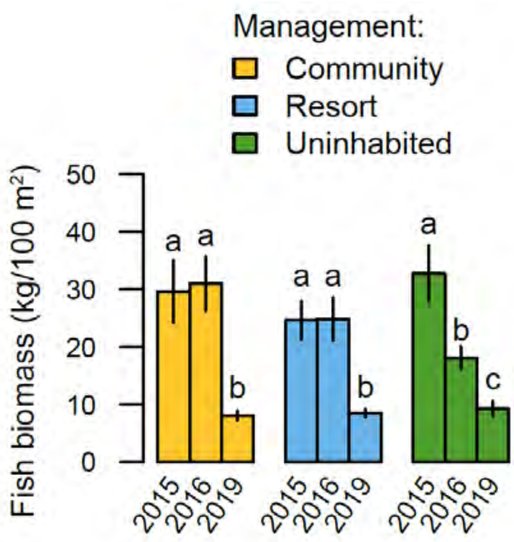


Figure 31. Mean fish biomass in 2015, 2016 and 2019 for community, resort and uninhabited islands. Vertical bars indicate standard errors. Different letters indicate significant differences between years.

Additional, evaluation of the data showed that a number of the reefs had transects with abnormally high biomass e.g. Rasdhoo, Kan'dholhudhoo, and Madoogali and variation between transects at the same site was sometimes remarkably high, e.g. Kan'dholhudhoo, Vihamaafaru. (Figure 33). This was usually attributed to the presence of schools of medium bodied fish and/or to a few large fish contributing strongly to the total biomass.

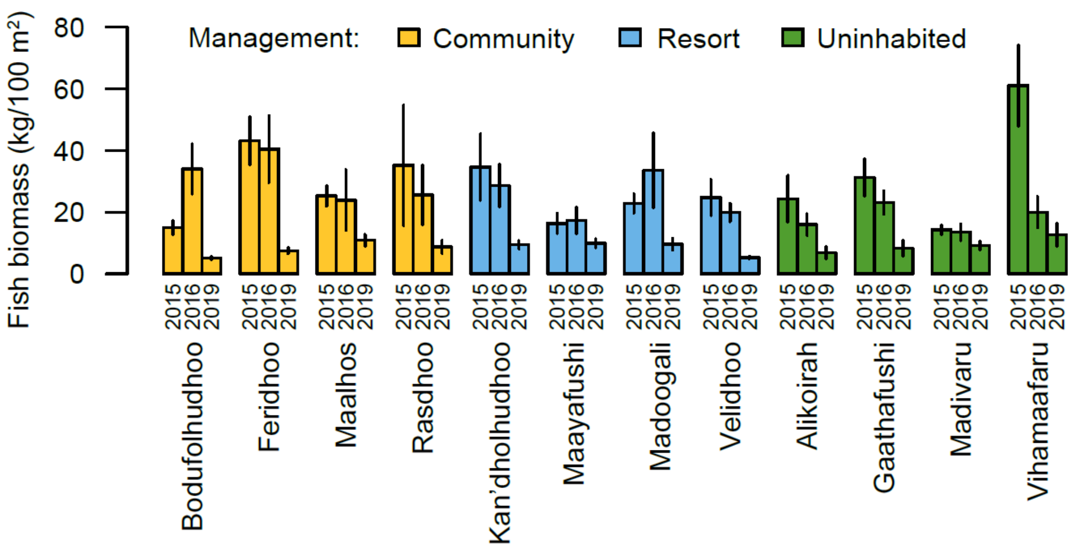


Figure 32. Mean fish biomass across the 9 transects surveyed at each island in 2015, 2016 and 2019. Vertical bars indicate standard errors.

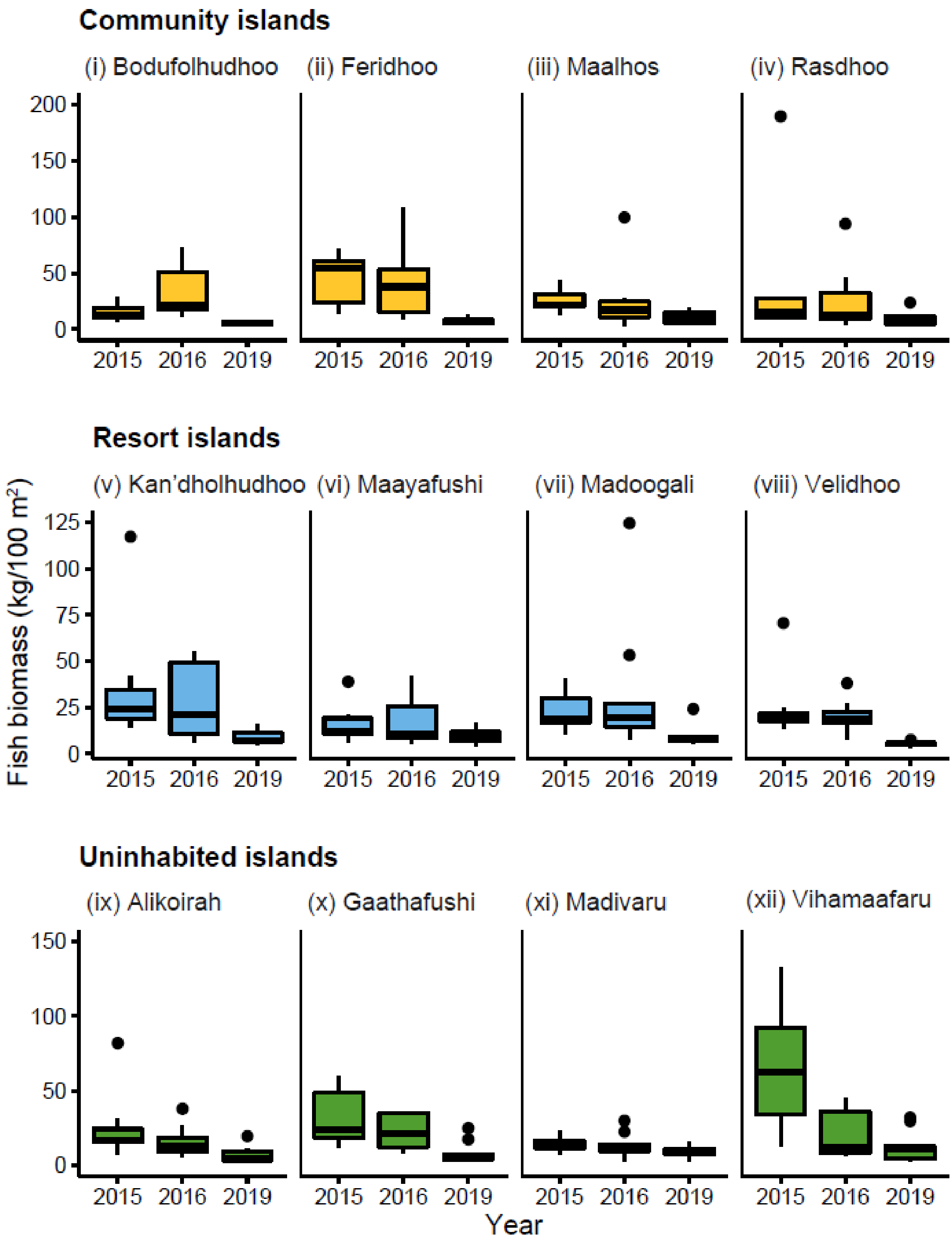


Figure 33. Fish biomass across the 9 transects surveyed at each island in 2015, 2016 and 2019.

Biomass significantly decreased over time for all groups investigated (Figure 34). For herbivores and coral-related fish species, biomass decreased significantly after 2015 (4.9 ± 0.3 kg/100 m^2 in 2015, 2.8 ± 0.5 kg/100 m^2 in 2016 and 1.1 ± 0.1 kg/100 m^2 in 2019 for herbivores; 5.2 ± 0.5 kg/100 m^2 in 2015, 2.7 ± 0.2 kg/100 m^2 in 2016 and 0.7 ± 0.04 kg/100 m^2 in 2019 for coral-related species), whereas it remained the same for carnivores, corallivores and planktivores in 2015 and 2016 before a significant decrease in 2019.

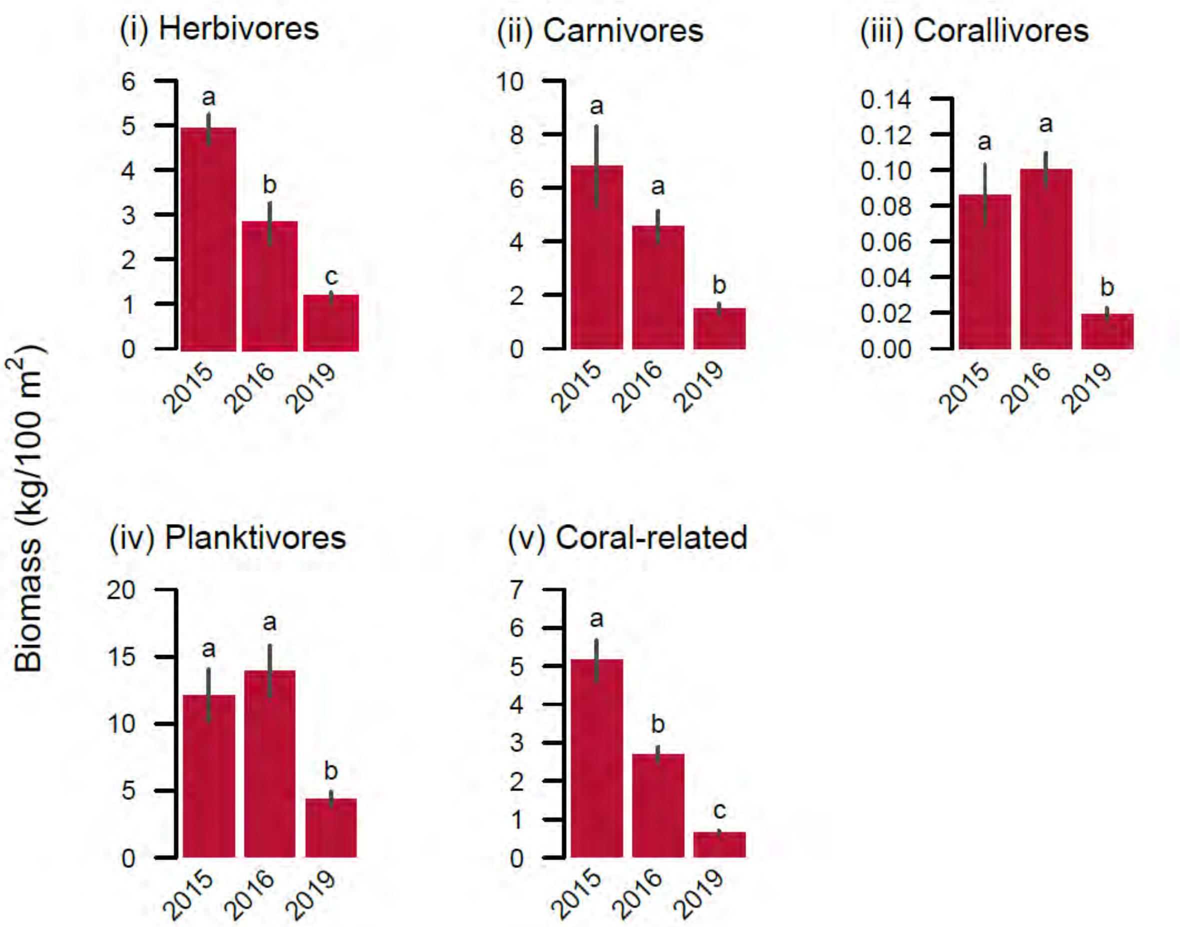


Figure 34. Mean (i) herbivore, (ii) carnivore, (iii) corallivore, (iv) planktivore and (v) coral-related fish biomass across the 12 islands surveyed in North Ari in 2015, 2016 and 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between years.

When separated into management regimes, biomass still decreased significantly for most groups across all management regimes in 2019 when compared to 2016 and/or 2015 (Figure 35). In some cases, (e.g. herbivores in community islands or carnivores in uninhabited islands) the decrease in 2019 was not significant due to the high variability in biomass values in 2015 and/or 2016 (Figure A2 1, Figure A2 2, Figure A2 3, Figure A2 4 & Figure A2 5). The community management regime was the only one where herbivores and coral-related species biomass did not decline significantly from 2015 (4.8 ± 0.6 kg/100 m^2 for herbivores and 3.9 ± 0.5 kg/100 m^2 for coral-related species) to 2016 (4.2 ± 1.3 kg/100 m^2 for herbivores and 2.9 ± 0.5 kg/100 m^2 for coral-related species). In contrast, the decline was particularly steady and strong for herbivores and coral-related species biomass at resort island reefs (from 4.3 ± 0.4 kg/100 m^2 in 2015 to 1.4 ± 0.2 kg/100 m^2 in 2019 for herbivores, and from 4.7 ± 0.5 kg/100 m^2 in 2015 to 0.5 ± 0.06 kg/100 m^2 in 2019 for coral-related species) and uninhabited island reefs (from 5.6 ± 0.7 kg/100 m^2 in 2015 to 0.9 ± 0.1 kg/100 m^2 in 2019 for herbivores, and from 6.9 ± 1.4 kg/100 m^2 in 2015 to 0.6 ± 0.09 kg/100 m^2 in 2019 for coral-related species). Carnivores showed a steady, but non-significant decline in biomass over the three years at the uninhabited island reefs, whereas on both community and resort island reefs, biomass of carnivores, corallivores, planktivores either increased or remained similar between 2015 and 2016 before declining in 2019.

A decline in biomass was observed in 2019 compared to 2015 and/or 2016 for all families and management regimes but was not necessarily significant (e.g. Acanthuridae and Siganidae at uninhabited island reefs) (Figure 36). The strongest significant decrease was observed for Scaridae, where a large drop in biomass was observed between 2015 and 2016 at for all management regimes. No other family presented a significant decrease in biomass between 2015 and 2016 regardless of the management regime. However, a significant decrease was observed in 2019, compared to 2015 and 2016, for Labridae in all management regimes and for Siganidae at resort islands, and Serranidae at resort and uninhabited islands.

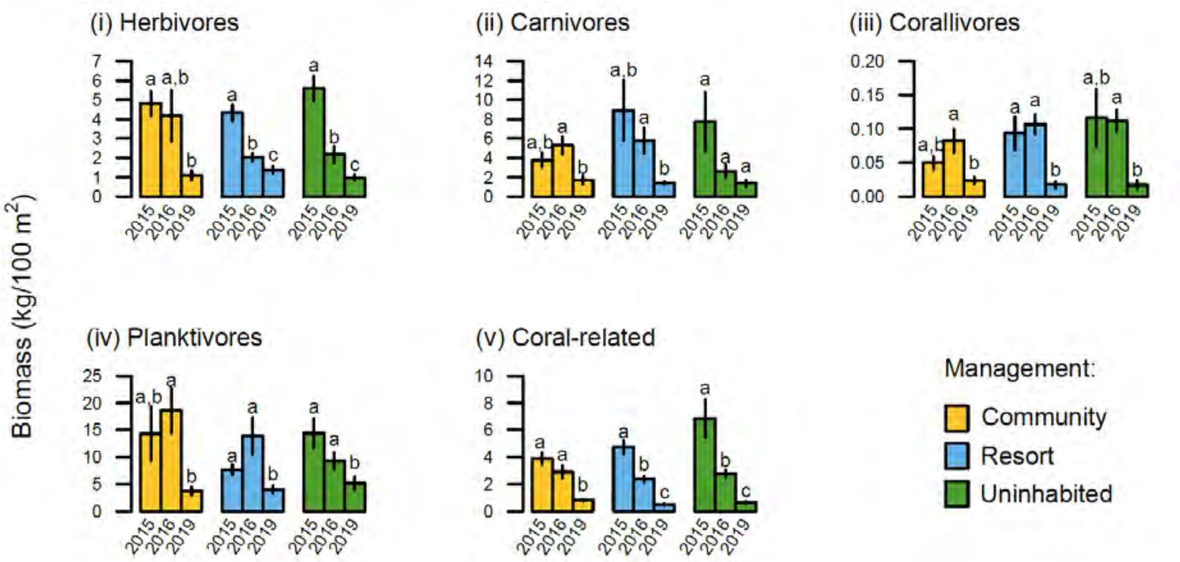


Figure 35. Mean (i) herbivore, (ii) carnivore, (iii) corallivore, (iv) planktivore and (v) coral-related species biomass in North Ari in 2015, 2016 and 2019 for community, resort and uninhabited island reefs. Vertical bars indicate standard errors. Different letters indicate significant differences between years.

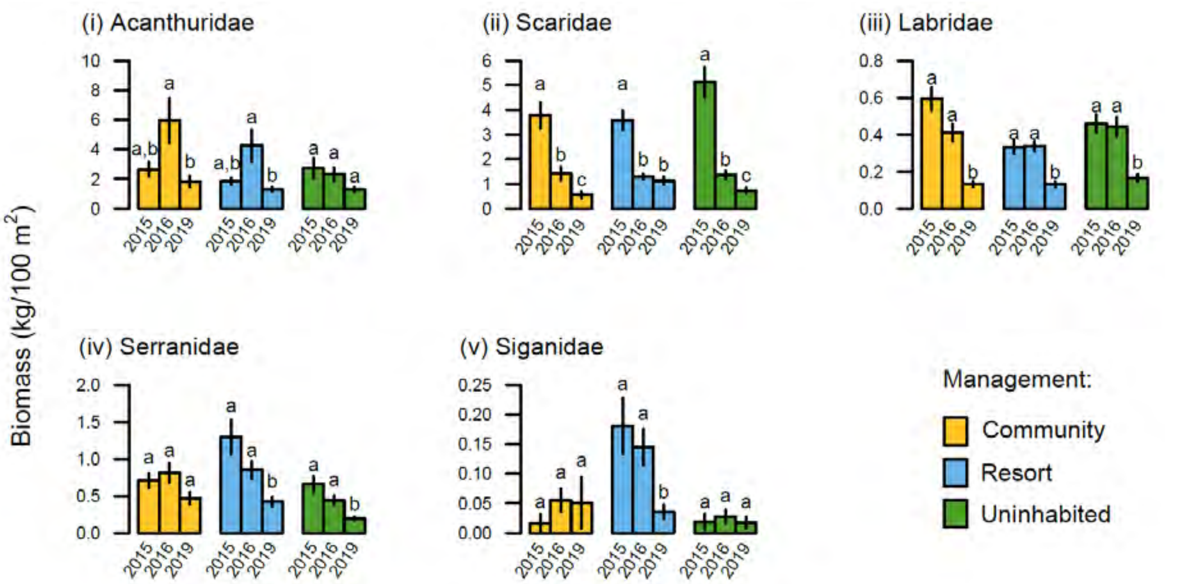


Figure 36. Mean (i) Acanthuridae, (ii) Scaridae (iii) Labridae, (iv) Serranidae and (v) Siganidae fish biomass in North Ari in 2015, 2016 and 2019 for community, resort and uninhabited island reefs. Vertical bars indicate standard errors. Different letters indicate significant differences between years

3.5.2. Fish community in 2019

Total fish density in the 12 sampled North Ari islands during the 2019 surveys was 322 (SE ± 31 /100 m^2) individuals per transect on average, diversity was 38 (± 0.75 spp/100 m^2) fish species per transect, and biomass was 8.6 ± 0.6 kg/100 m^2. Fish density (506 ± 70 /100 m^2) and diversity (42 ± 1.5 spp/100 m^2) were significantly higher at community island reefs, however there was no significant difference in biomass between the management regimes (Figure 37).

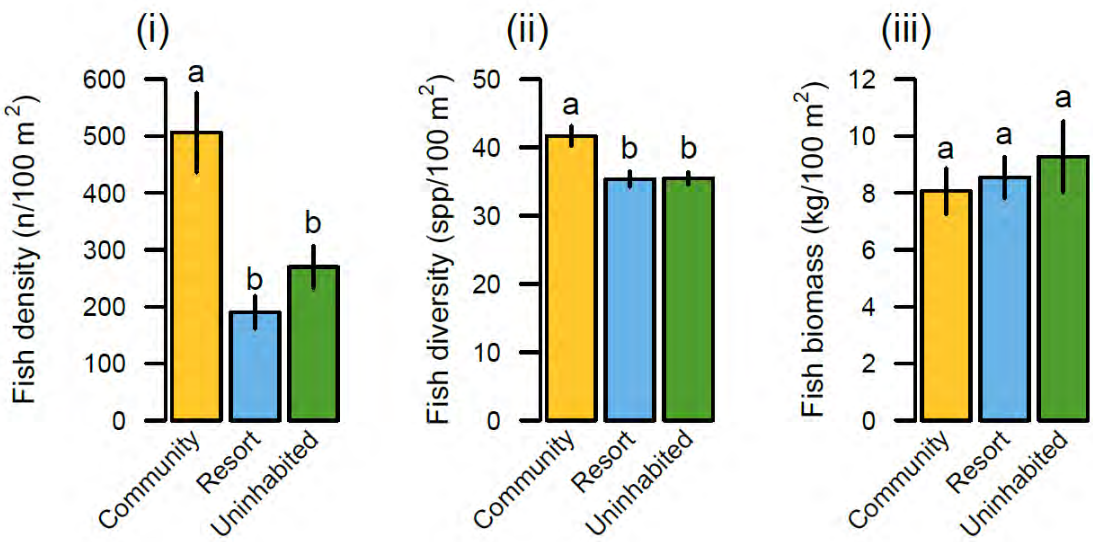


Figure 37. Mean fish (i) density, (ii) diversity and (iii) biomass across the three management regimes surveyed in North Ari in 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between management regime.

Fish density was especially high at Feridhoo (1077 ± 148 /100 m^2) (Figure 38), which resulted in fish density being significantly higher in community compared with resort and uninhabited island reefs. However, the high density did not result in a higher biomass at either Feridhoo or across the community island reefs, indicating that the fish community at these reefs was composed of small fish that contribute relatively little to overall biomass, such as anthias or chromis.

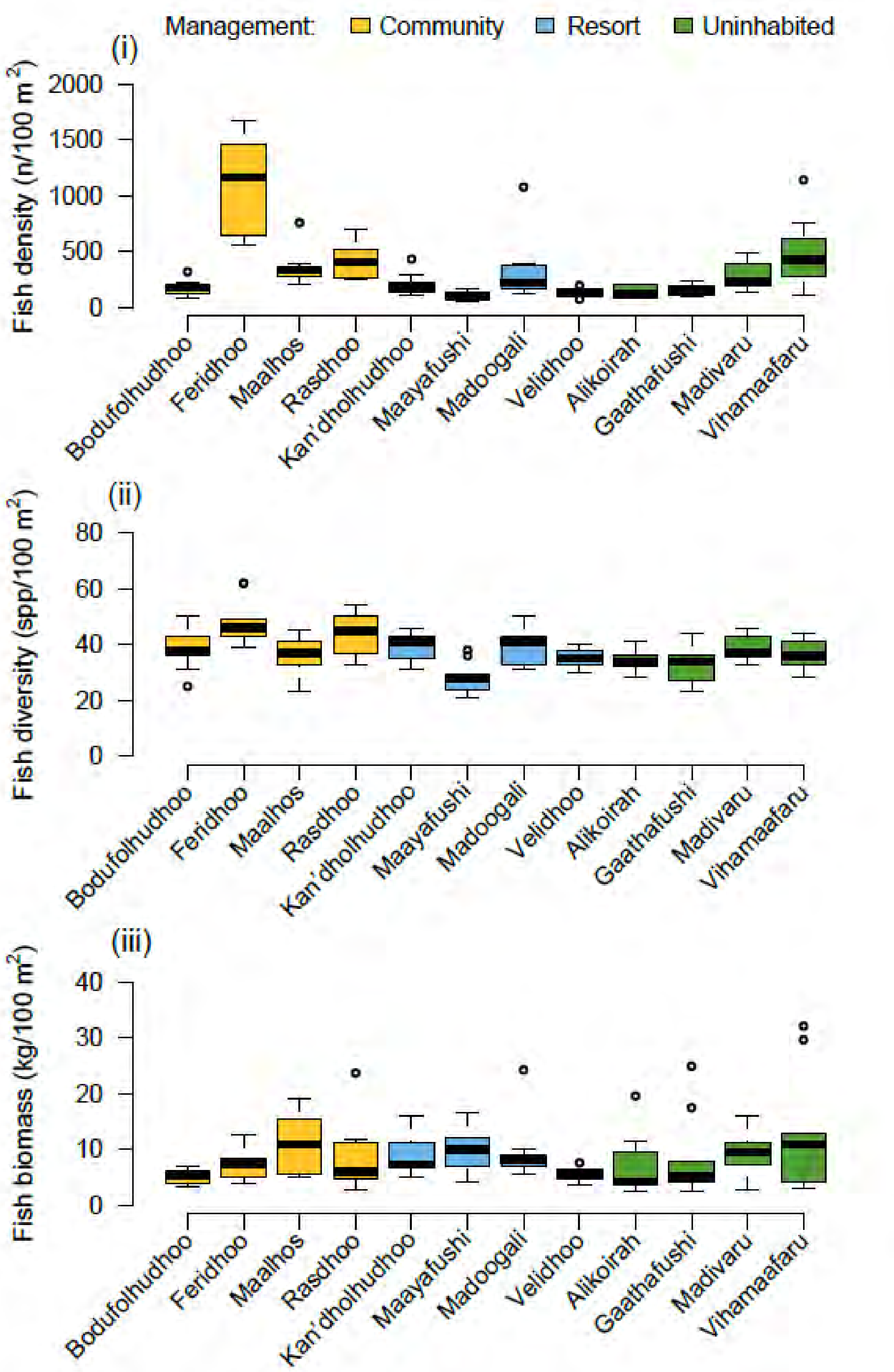


Figure 38. Total fish community (i) density, (ii) diversity and (ii) biomass at the 12 islands surveyed in North Ari in 2019.

Fish density (492 ± 52 ind/100 m^2), diversity (40 ± 1 spp/100 m^2) and biomass (9.8 ± 0.9 kg/100 m^2) were significantly greater at outer atoll reefs (Figure 39). The fish community here comprised high numbers of fishes of medium size, such as *Odonus niger, Myripritis adusta* and *Pterocaesio tile.* The highest biomass was found at Vihamaafaru (492 ± 52 /100 m^2) and Maalhos (10.9 ± 1.9 kg/100 m^2), both of which were outer atoll islands.

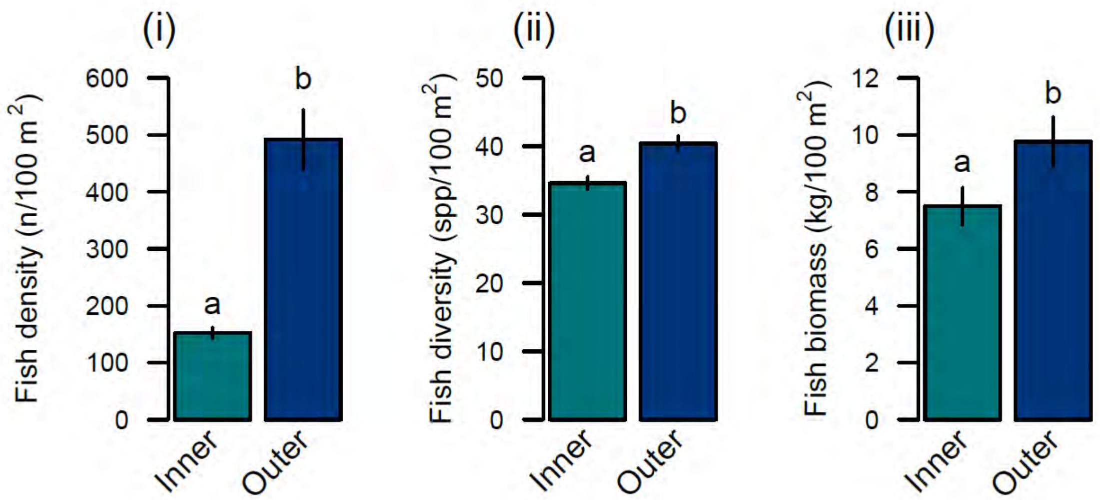


Figure 39. Mean fish (i) density, (ii) diversity and (ii) biomass at the inner atoll and outer atoll edge islands surveyed in North Ari in 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between exposures.

Herbivore biomass was 1.2 ± 0.1kg/100 m^2 on average over all islands. Trophic group biomass was similar at all management regimes (Figure 40), only coral-related species biomass was significantly lower in resort (506.6 ± 56.8 kg/100 m^2) compared to community islands (807.1 ± 71.3 kg/100 m^2).

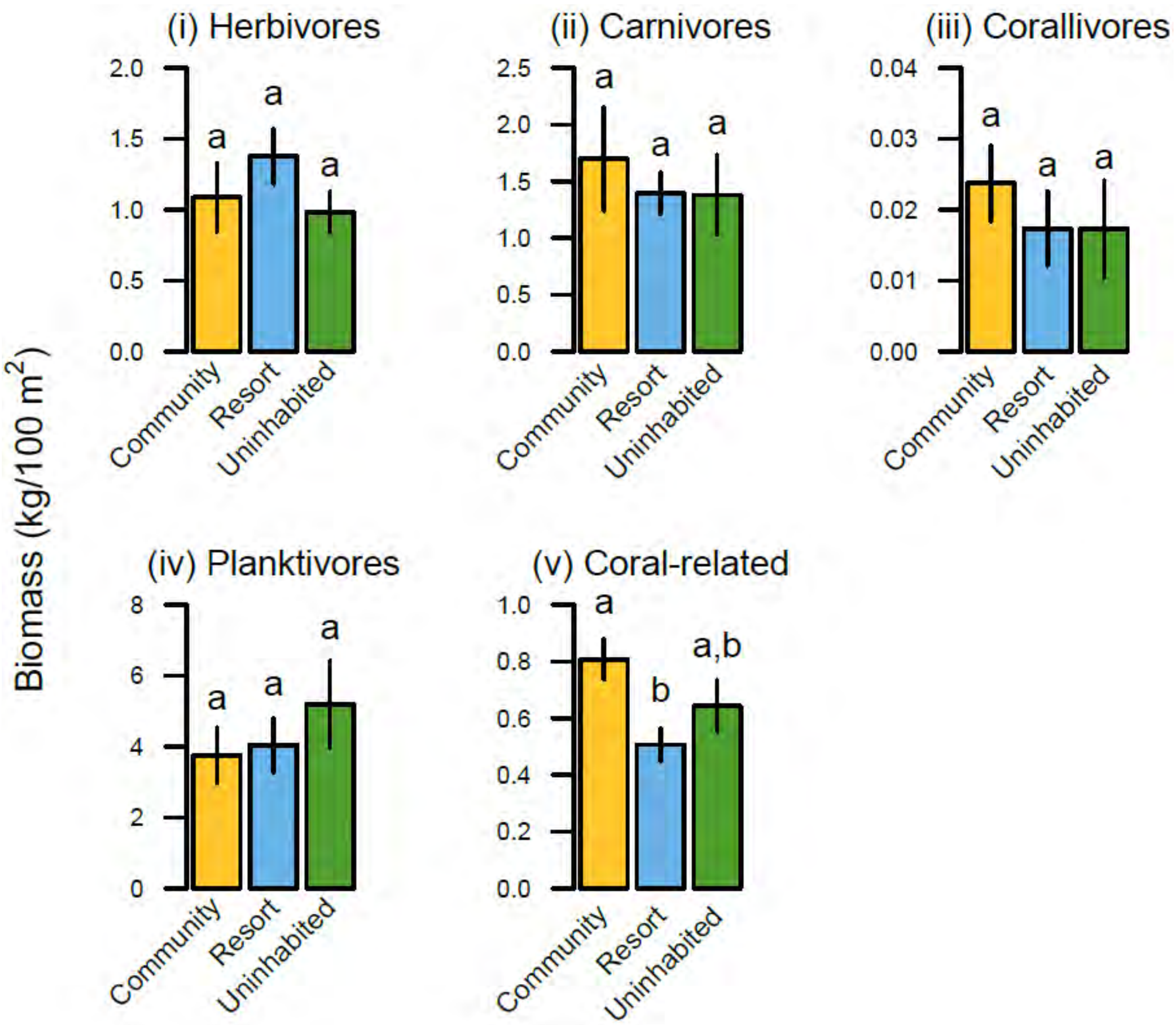


Figure 40. Mean fish biomass of (i) herbivore, (ii) carnivore, (iii) corallivore, (iv) planktivore and (v) coral-related species across the three management regimes surveyed in North Ari in 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between management regime.

Biomass of the groups was highly variable within and between reefs. Maalhos and Kan'dholhudhoo had the highest herbivore biomass (1.6 ± 0.8 kg/100 m^2 and 1.7 ± 0.5 kg/100 m^2, respectively). Carnivores were most abundant on transects at Maalhos (15.0 kg/100 m^2) and Madivaru (10.8kg/100 m^2) (Figure 41). This is likely to be where large Serranids or schools of Carangids were observed. Corallivores were abundant in Madivaru and present only in low numbers at Alikoirah and Gaathafushi. Planktivores were particularly abundant on some transects of Rasdhoo, Madoogali, Gaathafushi and Vihamaafaru. Alikoirah presented a transect with notably high coral-related species biomass.

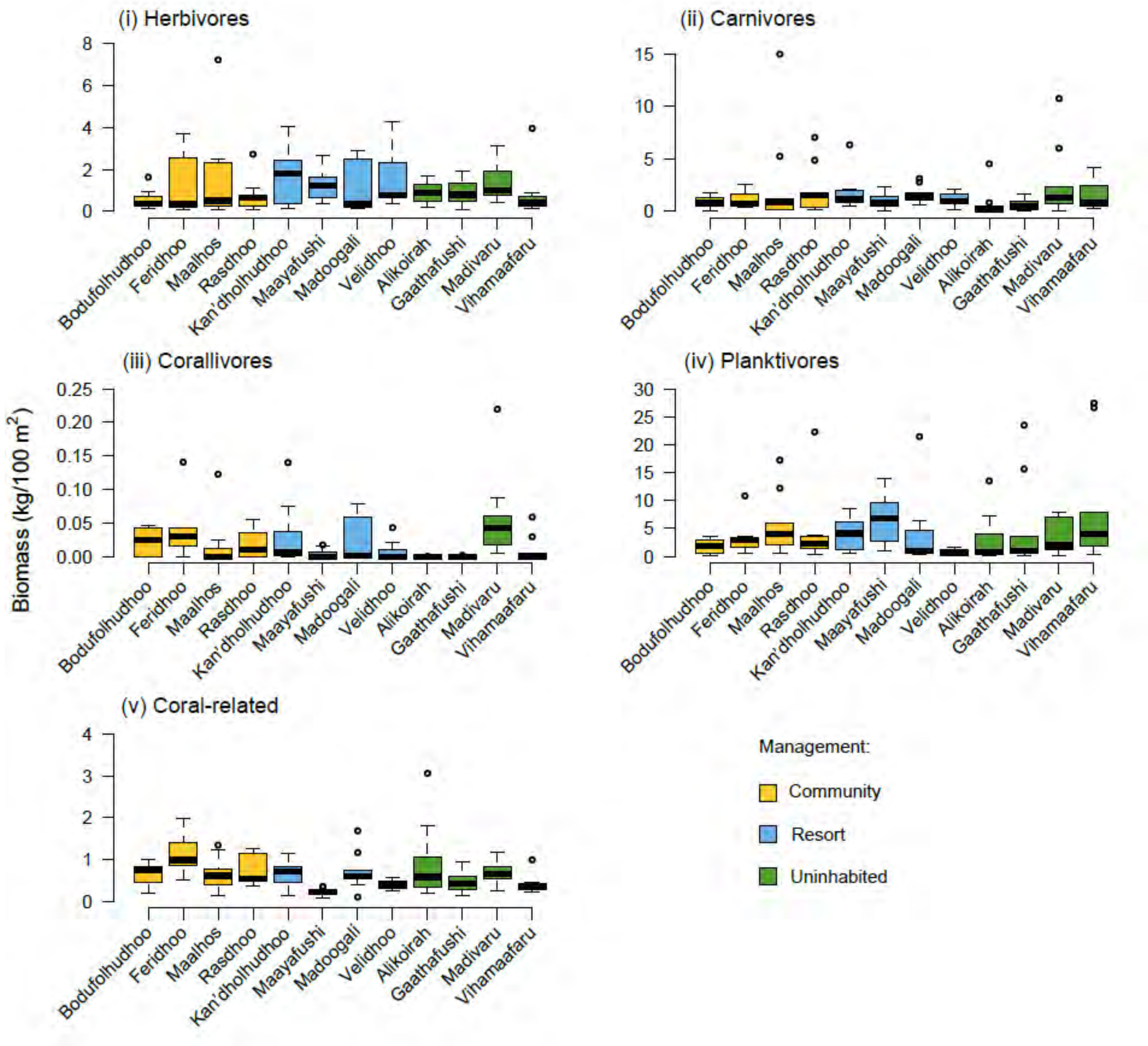
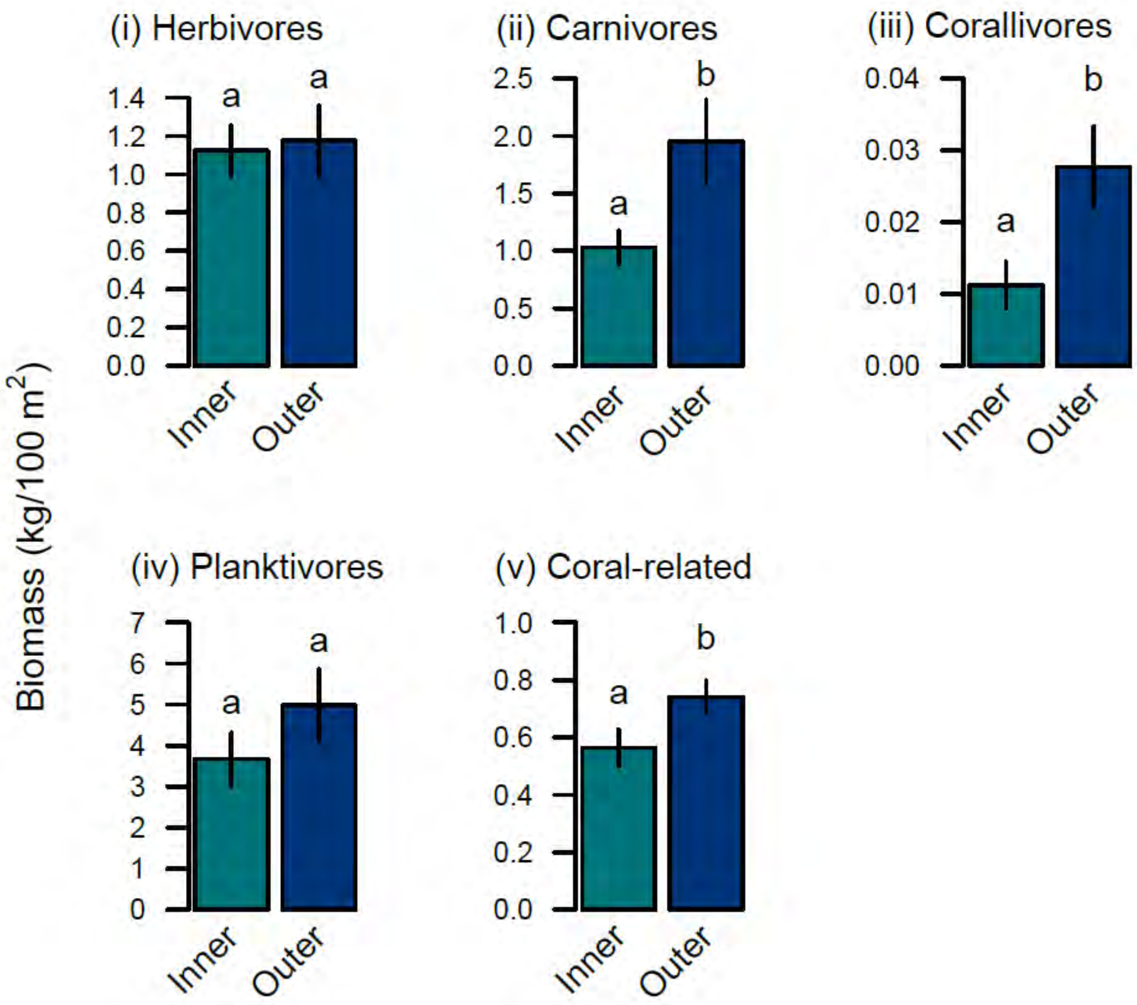


Figure 41. Mean fish biomass of (i) herbivore, (ii) carnivore, (iii) corallivore, (iv) planktivore and (v) coral-related species at the 12 islands surveyed in North Ari in 2019. Vertical bars indicate standard errors.

Biomass of carnivores, corallivores and coral-related species was significantly greater at the outer atoll reefs (**Error! Reference source not found.**). Herbivore and planktivore biomass did not significantly vary between either of the factors tested.



There were no significant differences between management regimes for the biomass of four of five families examined (Figure 43). Scaridae had a significantly lower biomass at community island reefs. Acanthuridae had a non-significantly higher biomass at community island reefs. Serranidae had a non-significantly lower biomass at uninhabited island reefs.

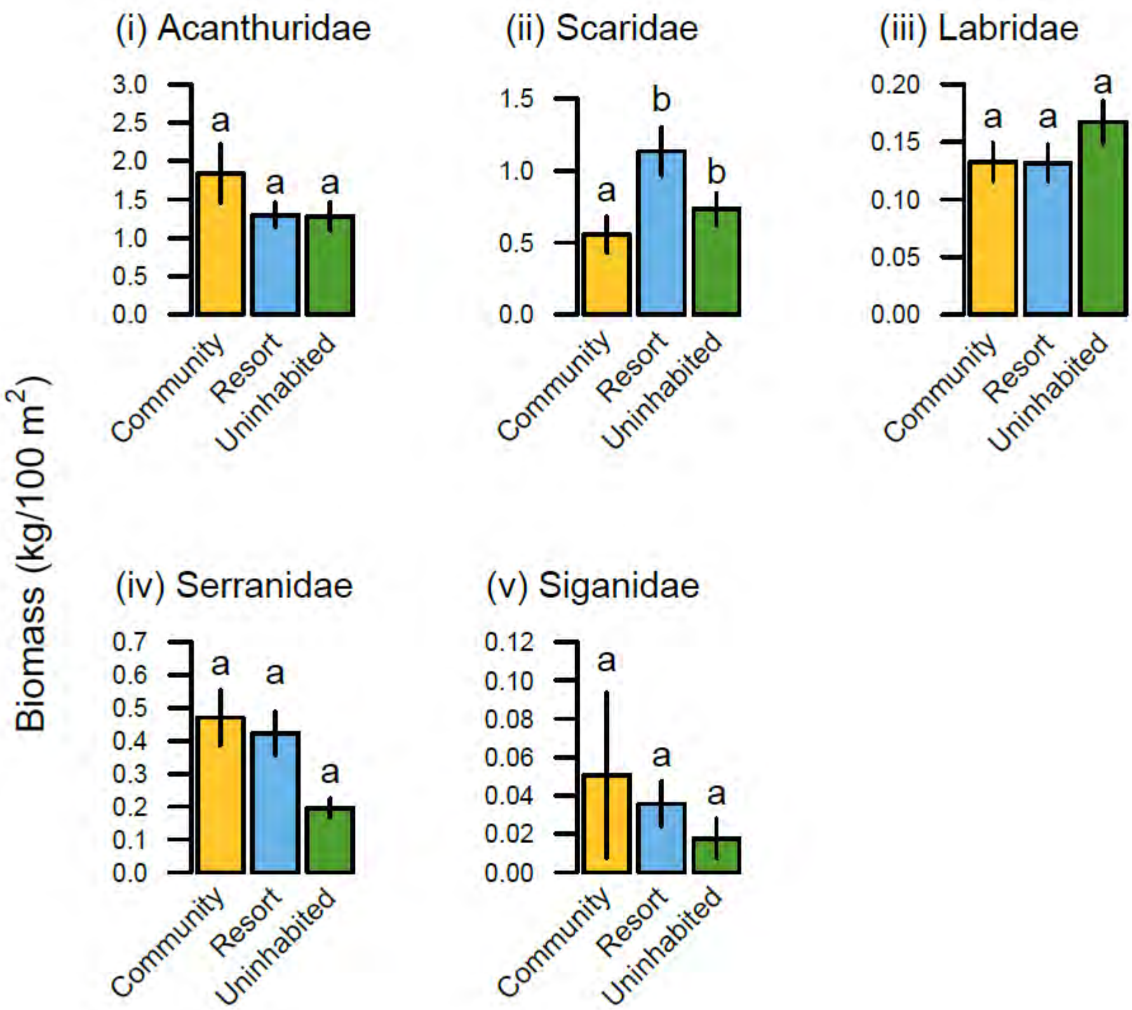
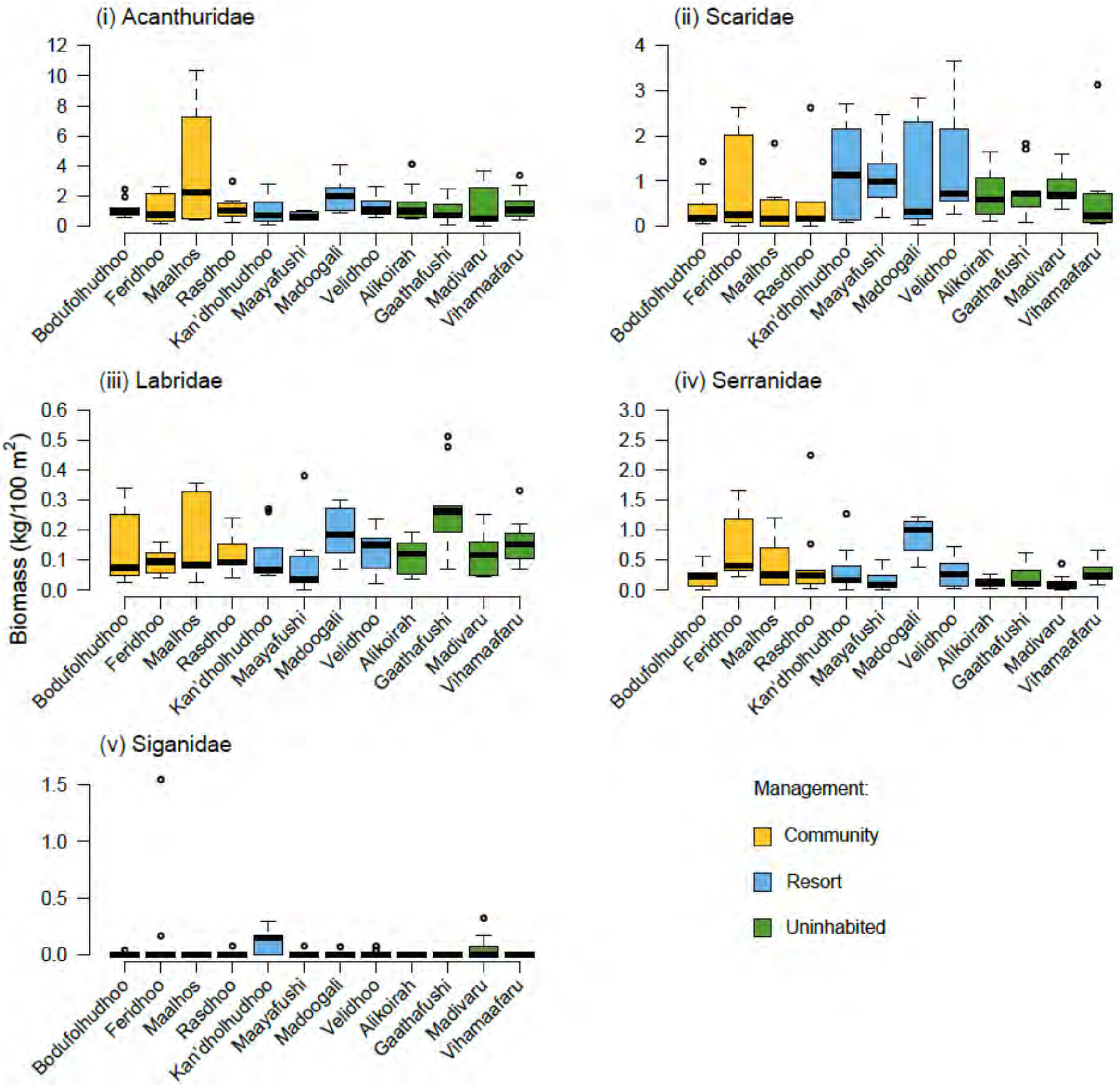


Figure 42. Mean (i) Acanthuridae, (ii) Scaridae (iii) Labridae, (iv) Serranidae and (v) Siganidae fish biomass across the three management regimes surveyed in North Ari in 2019. Vertical bars indicate standard errors. Different letters indicate significant differences between management regime.

There was high variability within management regimes and within reefs (**Error! Reference source not found.**). Scaridae had a significantly higher biomass at inner atoll reefs, whereas Serranidae had significantly higher biomass at outer atoll reefs (Figure 45).



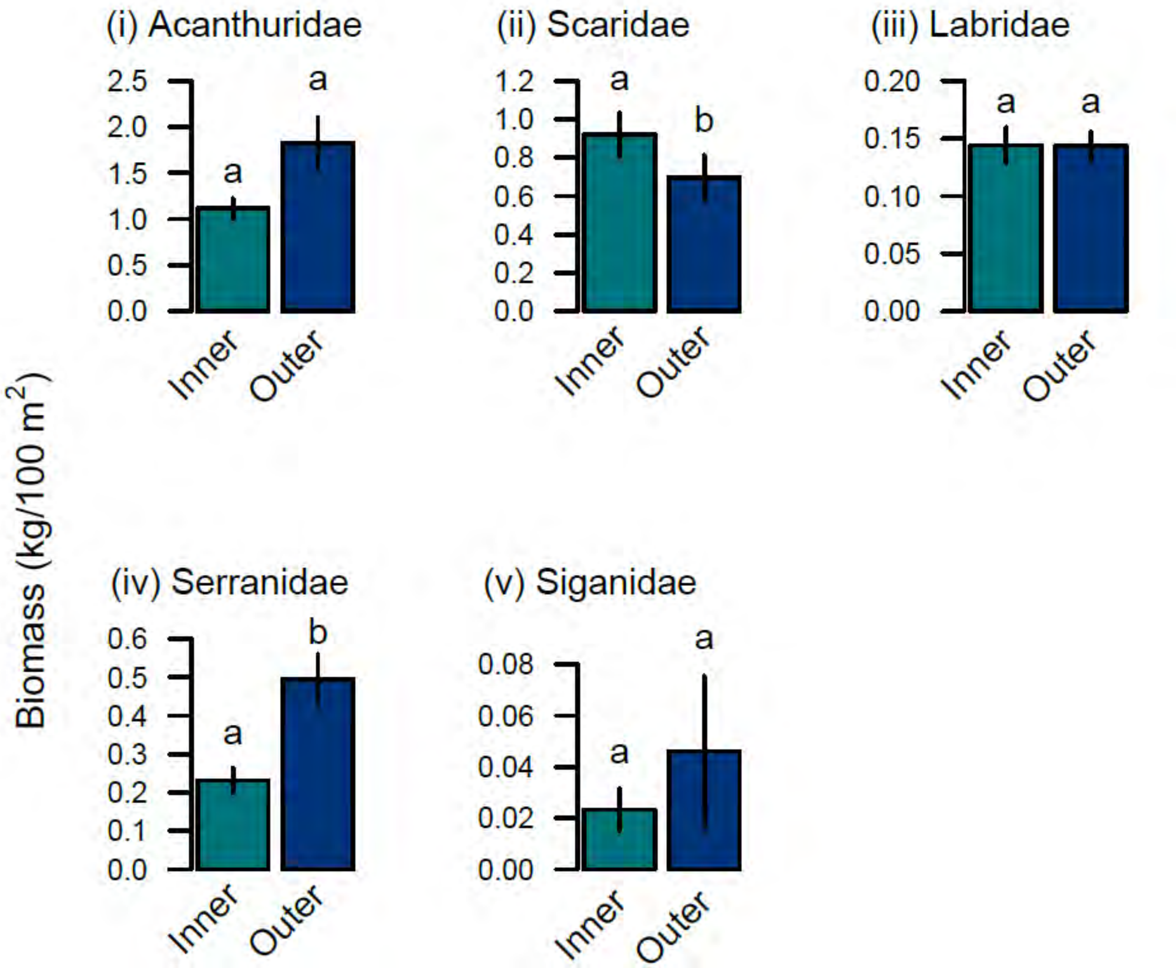


Figure 43. Mean (i) Acanthuridae, (ii) Scaridae (iii) Labridae, (iv) Serranidae and (v) Siganidae family biomass at the inner atoll and outer atoll edge islands surveyed in North Ari in 2019. Vertical bars indicate standard errors. Different letters ate significant differences between management regime.

3.6. Structural complexity and abiotic substrate

Structural complexity of reefs around North Ari Atoll declined significantly over the survey period (χ^2(df = 2) = 222.54, $p < 0.01$. There was no difference between reefs in 2015 and 2016 but complexity declined by 21.7 % (S.E. 1.33 %, df = 307.47, t = 16.31, $p < 0.01$) between 2016 and 2019.

During the baseline surveys, the median structural complexity was similar for uninhabited (median 29.8 IQR 21.1 – 36.5), resort (median 24.8 IQR 19.3 – 36.1) and community island reefs (median 29.5 IQR 22.2 – 37.4) and 25 or above for half of reefs (Figure 46, Table 16). Increases in complexity were observed between 2015 and 2016 for the uninhabited islands Alikoirah and Vihamaafaru. Increases in complexity were also observed at the resort islands Madoogali and Velidhoo. Reef structural complexity had also increased at the community island Feridhoo in 2016 but declines in complexity of the community reefs of Maalhos and Rasdhoo overshadowed this. The highest reef complexity was observed at Alikoirah (median 48.0 IQR 41 – 51.0).

Reef structural complexity declined at all reefs by 2019, following the coral mortality and subsequent breakdown of coral structure associated with the mass bleaching event in 2016. The declines in reef complexity occurred regardless of management regime and complexity was similar for community (median 10.5 IQR 4.75 – 15.0), resort (median 5.0 IQR 2.0 – 13.2) and uninhabited island reefs (median 6.5 IQR 3.0 – 12.2). The lowest complexity in 2019 was observed at the resort reef Maayafushi (median 0.0 IQR 0.0 – 1.0).

Outer atoll reefs had a significantly lower complexity than inner atoll reefs (χ^2(df =2) = 12.63, $p < 0.01$). Local exposure also had a significant impact on complexity with locally exposed reefs having significantly lower complexity than sheltered reefs (χ^2(df =2) = 7.89, $p < 0.05$). Complexity was 11.1 % (± 2.54 % S.E., df=297.67, t = 4.35, $p < 0.01$) lower on reefs that had a history of COTS presence.

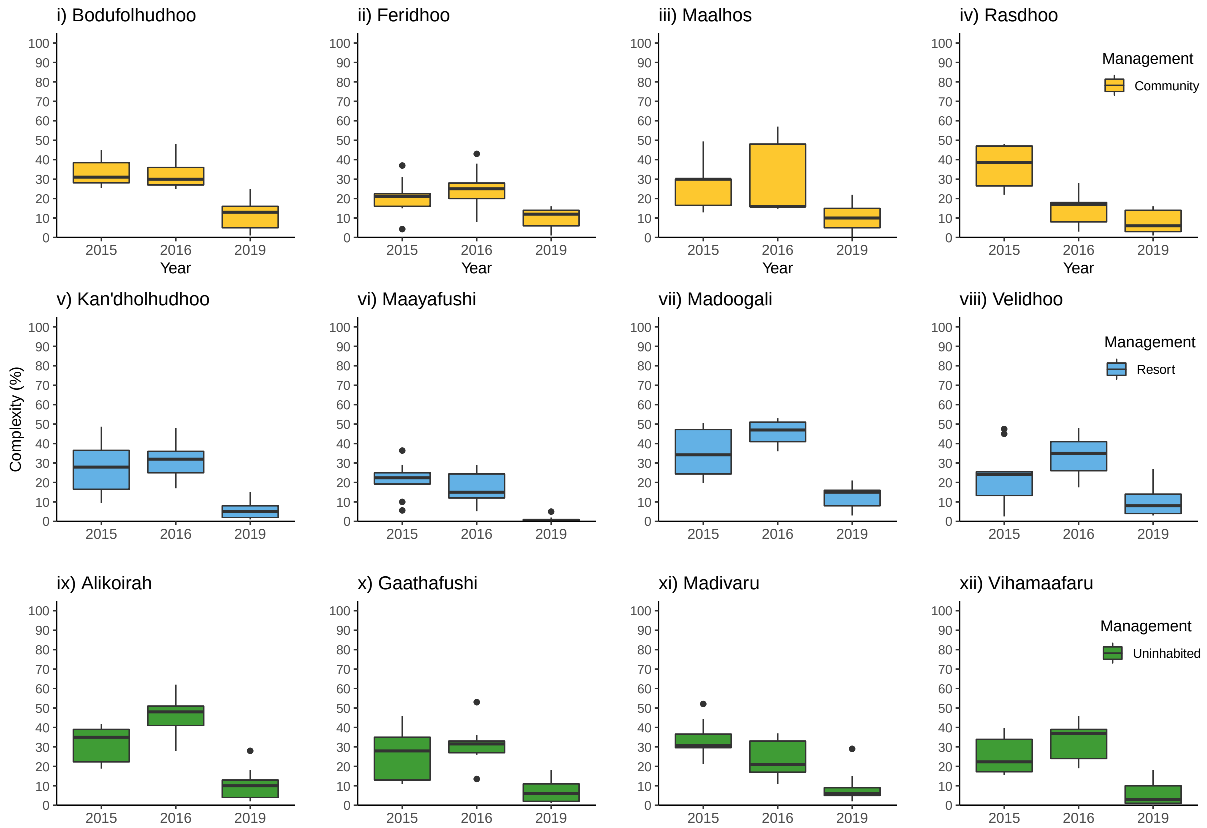


Figure 44. Reef complexity in 2015, 2016 and 2019 at the 12 islands surveyed in North Ari Atoll.

Table 16. Median and interquartile range (IQR) of reef complexity recorded on transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

		Year					
		2015		2016		2019	
Management	Island	Median	IQR	Median	IQR	Median	IQR
Community	Bodufolhudhoo	35.0	22.3, 39	48.0	41, 51	10.0	4, 13
	Feridhoo	27.9	13, 35	31.5	27, 33	6.0	2, 11
	Maalhos	30.7	29.6, 36.6	21.0	17, 33	6.0	5, 9
	Rasdhoo	22.3	17.2, 33.9	37.0	24, 39	3.0	1, 10
Resort	Kan'dholhudhoo	27.9	16.5, 36.5	32.0	25, 36	5.0	2, 8
	Maayafushi	22.4	19.2, 25	15.0	12, 24.4	0.0	0, 1
	Madoogali	34.2	24.4, 47.2	47.0	41, 51	15.0	8, 16
	Velidhoo	24.0	13.3, 25.5	35.0	26, 41	8.0	4, 14
Uninhabited	Alikoirah	31.0	28.1, 38.5	30.0	27, 36	13.0	5, 16
	Gaathafushi	21.2	16, 22.5	25.0	20, 28	12.0	6, 14
	Madivaru	30.0	16.5, 30	16.0	15.8, 48	10.0	5, 15
	Vihamaafaru	38.5	26.5, 47	17.0	8, 18	6.0	3, 14

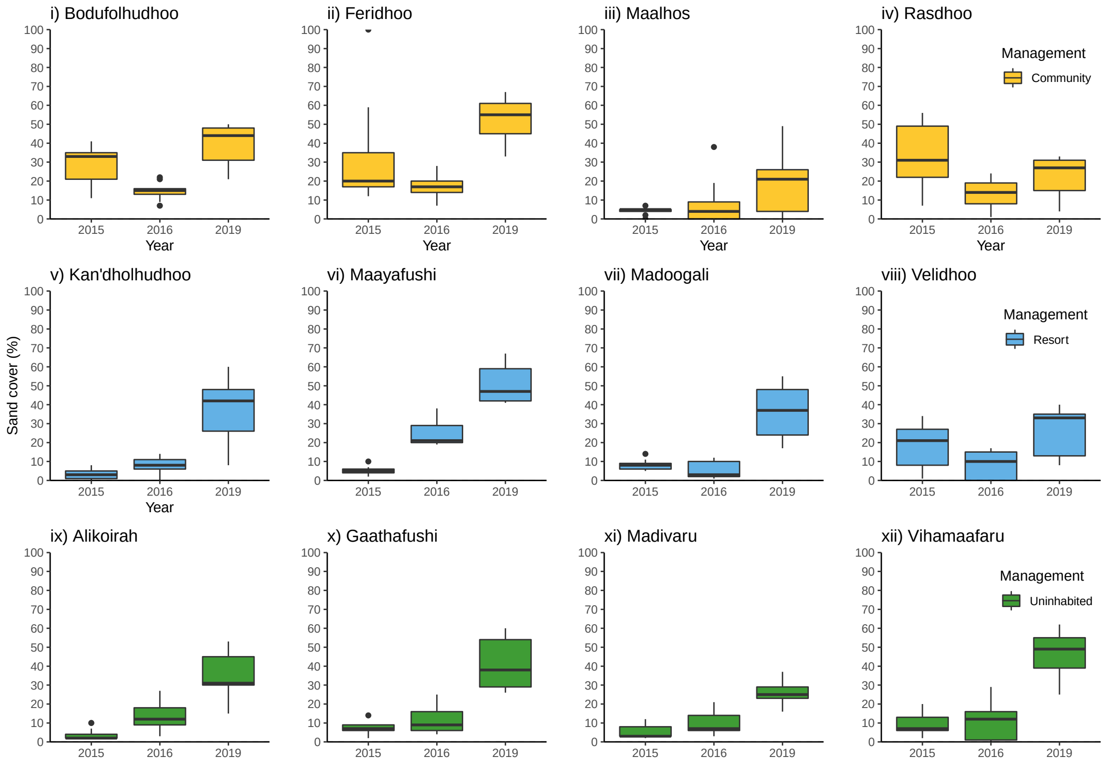


Figure 45. Sand cover in 2015, 2016 and 2019 at the 12 islands where PIT surveys were undertaken in North Ari Atoll.

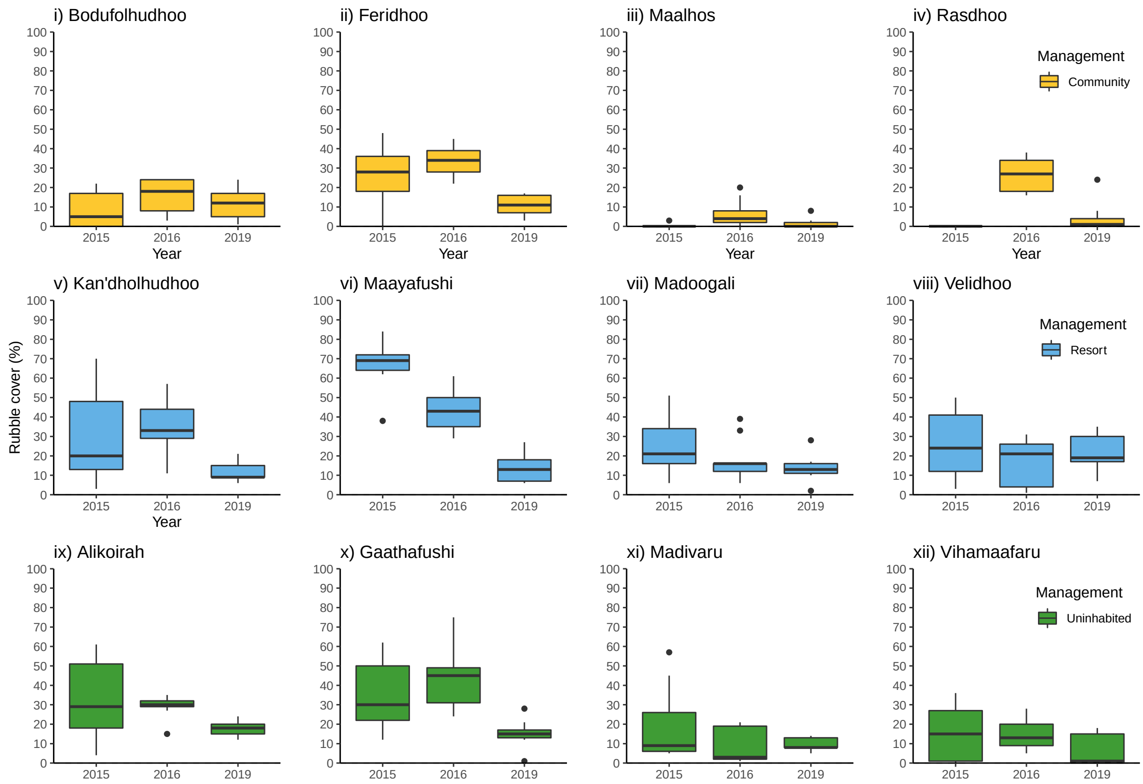


Figure 46. Rubble cover in 2015, 2016 and 2019 at the 12 islands where PIT surveys were undertaken in North Ari Atoll

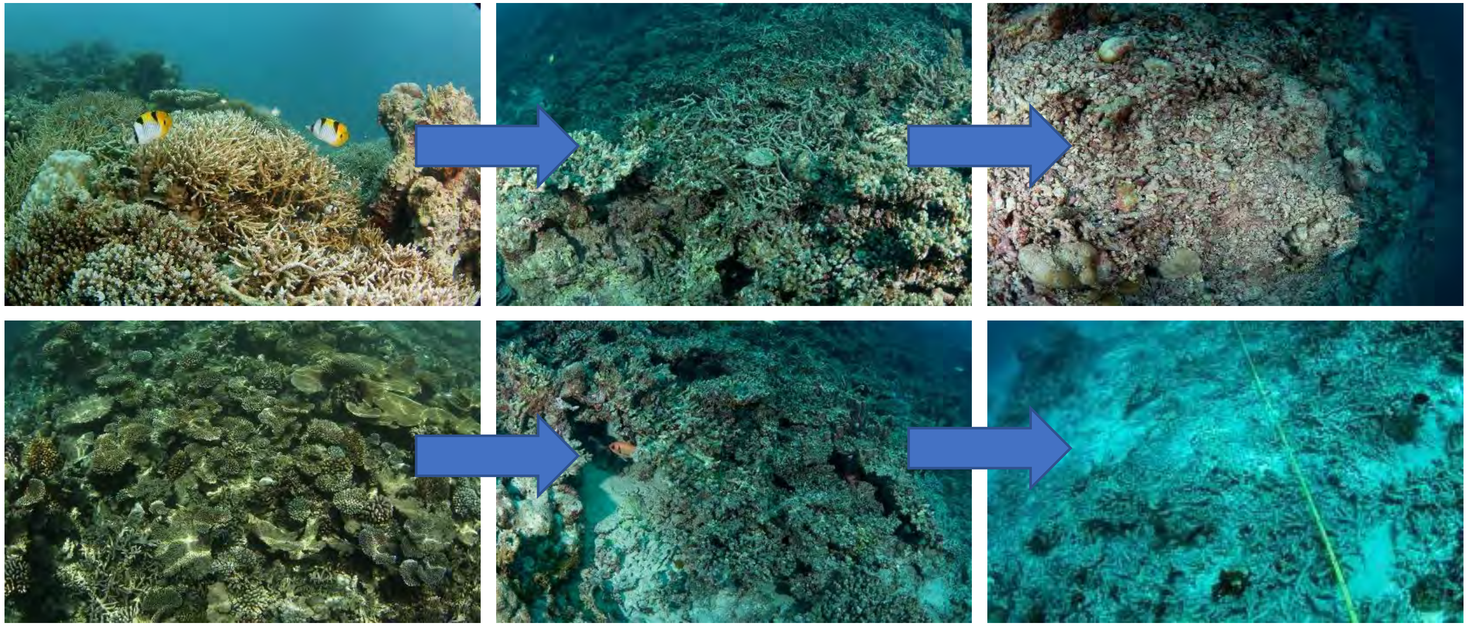


Figure 47. Decline in reef structural complexity from left: highly complex live coral structure to middle: medium complexity comprised of dead structure to right: low complexity dead rubble and sand.

3.7. Sea temperature data collected by IUCN at sites in North Ari Atoll.

Seawater temperatures briefly exceeded the proposed bleaching threshold temperature in May 2017, April 2018 and April 2019 (Figure 50). Surveys undertaken in June 2019 observed minor bleaching, which would suggest the bleaching threshold is accurate. No surveys were undertaken in 2017 and 2018 to confirm or record bleaching reports. It is likely that temperatures at 10 m depth in North Ari Atoll exceeded the proposed bleaching threshold temperature of 30.9 ˚C in the months of April and May in 2016 when the mass bleaching event was observed.

Temperatures at 10 m depth generally range between 27 ˚C and 31 ˚C. Records since June 2016 indicate that the coolest months of the year are January and February. The coolest temperatures recorded (~ 26.3 ˚C) where in January 2017. Temperatures in 2018 January and February were relatively high. The warmest months of the year in the records reported here are March, April and May.

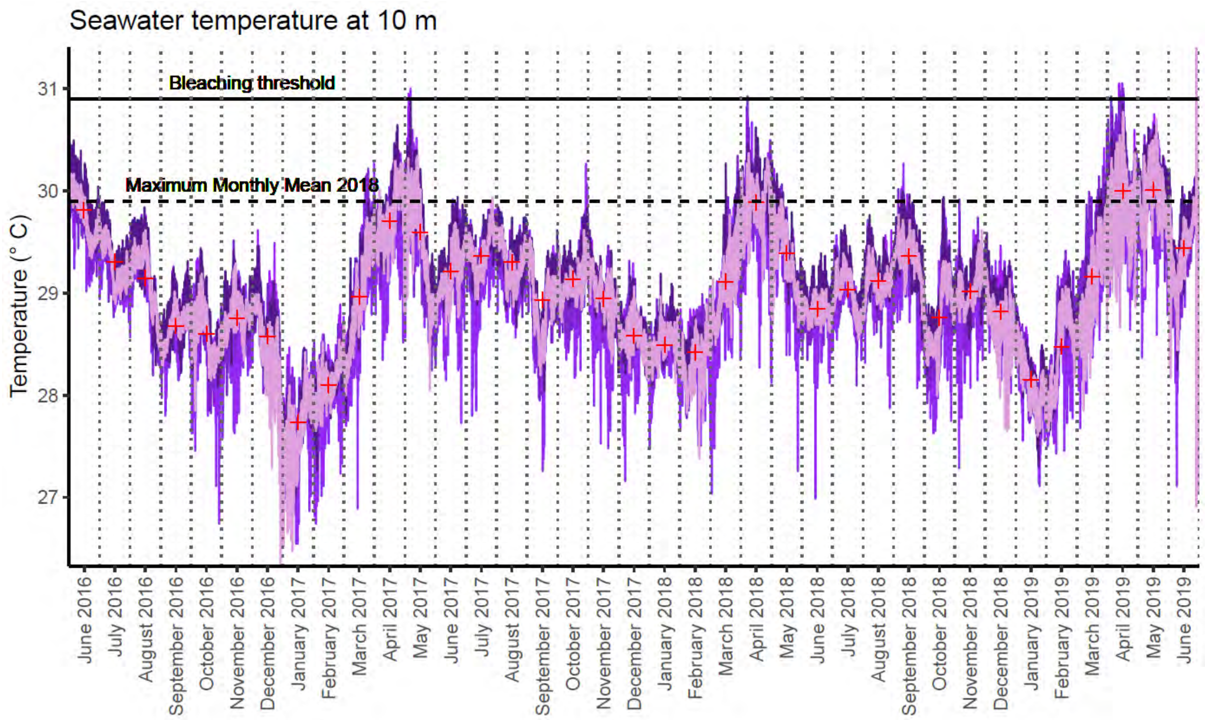


Figure 48. Sea surface temperatures at 10 m with Hobo Onset loggers.

4. Discussion

The 2016 mass bleaching event resulted in a decline in coral cover, coral diversity, lower coral recruitment, reduced fish biomass and declines in the key fish groups. Reefs have undergone a severe decline in structural complexity that has resulted in flattening of reef habitat and a reduction in the three-dimensional reef matrix which is vital in supporting diverse reef assemblages. The structural degradation has been accompanied by an increase in the proportion of reef substrate comprised of sand and a subsequent decline in suitable solid habitat for settlement or growth of corals. The reef fish community has suffered corresponding declines in density, diversity and biomass. These impacts were noticeable across all fish groups and families examined. Management regime appears to have had little effect in limiting the negative consequences of the bleaching event. There was some difference in post-bleaching trajectory between islands. This was dependent on the specific physical, biological and social characteristics of the island. Outer atoll reefs appeared to be in a healthier condition than inner atoll reefs. Islands with evidence of recent COTS outbreaks were already in a degraded state at the start of the surveys which was compounded by the effects of the bleaching.

Figure 49. Bleached corals during the 2016 surveys

4.1. Substrate cover

There has been a severe decline in coral cover driven by the bleaching event. The impact of the bleaching masks any potential management effect in this study. However, the analysis does suggest that impact of management may be influenced by island location, where outer atoll resort reefs appear to have higher coral cover, though this finding is not conclusive. Turf algae remained consistently high (approximately 25 – 30 % of substrate cover) across years, management and environmental gradients. Turf algae cover would be expected to increase following coral loss. Dead corals are quickly colonised by turf algae (Diaz-Pulido and McCook 2004, Diaz-Pulido et al. 2009). However, this was not the case here and it may be that grazing by herbivores numbers prevented this. If this is the case, then the decline in herbivores observed during the fish surveys may be a concern as fewer herbivores may allow turf algae grow unabated. High cover of turf algae has negative implications for the recruitment of corals and other benthic organisms (Birrell et al. 2005). Turf algae increase retention of sand and other particulate matter on a reef substrate.

CCA may have been impacted by the bleaching as it is susceptible to bleaching due to higher water temperatures (Latham 2008) under higher light stress, particularly under calm water conditions during a coral bleaching event (Irving et al. 2004). It is possible that inner island reefs are more susceptible to stresses associated with management (e.g. increased sediments or sand, pollution or waste disposal). In which case this strengthens the argument that management should be more cautious on inner islands compared to outer islands. Sediment (sand) (Fabricius and De'Ath 2001) and turf algae can combine to smother CCA (Steneck 1997), both of which now make up a significant proportion of the substrate in North Ari. Macroalgae increase in 2016 could relate to reduced coral cover due to greater space and reduced competition. Though macroalgae cover was generally very low and there was no further increase from 2016 to 2019 which would be expected if the reefs were undergoing a phase shift following the bleaching event (Ledlie et al. 2007).

Since 2016 there has been an approximate 30 % increase in the proportion of the reef substrate that is occupied by sand at North Ari Atoll. An increase in sand of this magnitude is consistent with the degradation of a reef community, widespread mortality of corals and progressive erosion of the structure built by corals and other calcareous organisms structure (Schuhmacher et al. 2005, Lasagna et al. 2010). The most serious implication of a greater proportional cover of the substrate by sand is the reduction in suitable habitat for benthic organisms. Coverage of the substrate by sand and other particulate matter such as silt and sediment reduces the substrate that is suitable for the recruitment of corals and other benthic organisms (Birrell et al. 2005, Cameron et al. 2016). It is possible that the lower abundance of coral recruits on reefs in North Ari Atoll after 2016 is in part a result of higher levels of sand on these reefs following the bleaching event in 2016.

Dead corals breakdown and their erosion has produces sand, which now occupies a considerable amount of the reef substrate at 10 m on the reef slopes. It may be expected that this sand is gradually transported off the reef (Hughes 1999) and that in time as the amount of dead coral left to erode declines the amount of sand will decrease. The results suggest that the management of reefs does not influence the amount of sand. However, it is important to emphasise that this our data is relevant to at 10 m depth and primarily reef slopes. It possible that sand remains longer on reef flats or accumulates at the base of a reef slope. It may be expected that sedimentation may be higher around resort reefs where beach replenishment through sand pumping is common. No effect of management was found here which may indicate the resorts in our data are managing their dredging and artificial beach programs responsibly. It may have been expected that the widespread mortality of coral observed here would have resulted in a subsequent increase in the proportion of rubble on reefs however, this was not the case. It may be that rubble is rapidly transported of reef slopes in the Maldives (Hughes 1999) or that the rubble has been eroded and has contributed to the significant increase in sand cover.

Acropora are among the most sensitive coral genera to coral bleaching (Baird and Marshall 2002, McClanahan et al. 2004). This is supported by our observations that cover of *Acropora* declined from 2015 to 2016 and further from 2016 to 2019. *Porites* is less susceptible to bleaching than *Acropora* (McClanahan 2004). This may be why no difference in percent cover of *Porites* was detected between years. *Pocillopora* is considered to be susceptible to bleaching (McClanahan 2004), yet there was no significant difference in percent cover of *Pocillopora* between years. *Pocillopora* has a generally low presence on reefs in the Maldives given the genus was severely affected by bleaching in 1998 (McClanahan et al. 2004). Having a generally low percentage cover or being relatively rare may have made it harder to detect changes in the cover of Pocillopora between years. Alternatively, it may be that because *Pocillopora* is a brood spawner, meaning it reproduces year round, this genus may have been able to recover more quickly following the bleaching event. Temperature can act as a driver for reproductive plasticity in *Pocillopora*, potentially enhancing individual success under fluctuating conditions (Crowder et al. 2014). *Pavona* is considered to be moderately resistant to bleaching (McClanahan 2004), yet was a significant difference in percent cover of *Pavona* between years. Cover of *Pavona* was generally low, with most islands having a median cover of 0 % in both 2015 and 2016. By 2019 *Pavona* was absent from all but two islands, Madivaru and Madoogali.

The cover of *Acropora* was highest on resort island reefs and lowest on community island reefs. It may be that that stresses from human activity on community island reefs may be resulting in lower *Acropora* cover. Resort and uninhabited island reefs appear to be more favourable and presumably less stressful to *Acropora* and so have a higher percentage cover. The higher *Acropora* cover at the lower energy environments, such as sheltered reefs and inner island reefs, favour the development of larger more delicate coral morphologies. This may have resulted in higher *Acropora* cover, e.g. coral tables and larger stands of branching corals. The species composition of *Acropora*, not detailed in our data, is likely to shift towards more sturdy and diminutive growth forms in higher energy environments such as outer islands and exposed reefs (Veron 2000).

Pocillopora were more abundant on high energy outer atoll island reefs. This may be because they naturally favour this habitat or because these reefs were less susceptible to bleaching (i.e. more water movement, and more wave action, kept temperatures and light intensity lower). The low cover of *Pavona* makes it challenging to draw strong conclusions about the drivers behind its distribution. However, *Pavona* was noted to occur more commonly on outer atoll reefs

Reef slopes were a favourable habitat for *Acropora* and percent cover of *Acropora* was higher on slopes. Terrace habitats are likely to have been stressed more than slopes and walls during the bleaching event (see bleaching results). Walls are mostly suitable for side attached *Acropora* tables which reduces the diversity of *Acropora* and the likelihood of high *Acropora* cover.

Porites cover was lowest on terrace reefs. Terrace habitats are unfavourable to coral during bleaching events. These upward facing habitats are likely to be stressed for more hours in the day by light during a bleaching event. When a coral bleaches, high temperatures result in a break-down of the photosynthetic pathways in the zooxanthellae pigments, if the pigments continue to receive energy from sunlight an already detrimental process is forced to keep working (Morrow et al. 2018).

Local environmental conditions alter the impacts of management on the percent cover of *Porites*. This interaction was found elsewhere in this study and suggests the impact of human action being greater in calm and sheltered conditions. This may be related to, or result from the bleaching event, which would most likely impact corals more in calmer conditions. Local exposure has a stronger effect than island location in altering the effects of management. The interaction of management and exposure is also indicates of less impact of management on outer reefs where the influence of more dynamic environmental conditions may outweigh any management affects.

COTS feed preferentially on *Acropora* relative to other coral genera (Pratchett 2007). Therefore, it is not surprising that there is lower cover of *Acropora* on the reefs in North Ari Atoll where COTS have been observed in the surveys. However, there was no relationship between COTS and the other three common genera. *Porites* and *Pavona* colonies are amongst the corals least preferred by COTS (De'ath and Moran 1998, Pratchett 2007). Despite a preference for *Pocillopora* (Pratchett 2007) by COTS, colonies are commonly inhabited by symbiotic crabs that aggressively defend the corals against COTS (Pratchett 2001).

COTS outbreaks are the most likely causes of lower coral cover on reefs at Alikoirah and Gaathafushi in 2016 and are also likely to have contributed to progressive declines in coral cover at Kan'dholhudhoo and Maayafushi. Interestingly, Alikoirah, Gaathafushi and Kan'dholhudhoo were amongst the reefs that experienced relatively large increases in macroalgae cover in 2016. Macroalgae are reported to compete for space with corals (McCook 2001, Hughes et al. 2007) and thus the early coral mortality associated with bleaching in 2016 may have facilitated macroalgae dominance. However, the results reported here raise the questions of whether COTS outbreaks facilitate greater dominance of macroalgae, and bleaching disturbances facilitate greater dominance of turf algae. Increases in Macroalgae are associated with reduced removal of macroalgae biomass by herbivores (Hughes 1994, Hughes et al. 2007). However, the abundance of herbivores can also increase, at least temporarily, as a result of greater food availability associated with higher macroalgae cover (Pratchett et al. 2018)


Figure 50. COTS feeding on coral.

4.2. Fish community

The bleaching event appears to have had severe impacts across the entire fish community, with total biomass and fish density dropping approximately 70 % and 50 %, respectively, between 2015 (before bleaching) and 2019. There were some similarities and differences in the islands between 2015 and 2016 which may be a result of the immediate impacts of the bleaching, as bleached corals are still able to provide many essential ecosystem services to the majority of fish species such as food and three-dimensional structure. However, by 2019, three years after the bleaching event, many corals were dead, and their structure was greatly altered. This has strongly impacted the fish community across most groups. Management regime appears to have had little if any effect on the overall condition of the fish community, suggesting the impact of bleaching may have been stronger than any recent human pressures. The biomass dropped so dramatically everywhere that it is difficult, at present, to determine any differences across the surveyed islands that could be attributable to anthropogenic pressures. Surveys showed almost every facet of the fish community declined to comparable levels by 2019 regardless of the management regime.

The three-year gap between the 2016 and 2019 surveys prevents us from understanding the short-term response of the fish community following the bleaching, though studies have shown it can take time for the damage of the bleaching event to permeate the fish community(Graham et al. 2007, Alvarez-Filip et al. 2009, Lamy et al. 2015). Species dependent on the coral structure tend to show a delayed response to bleaching events. The erosion of the reef structure following coral mortality, reduces the habitable space on reefs for these species (Graham et al. 2009). The immediate impacts of the bleaching event may not have been apparent throughout the fish community during or immediately following the bleaching as most reef fish are not dependent on live coral for resources (Lamy et al. 2015). Long-term declines in fish biomass following bleaching are known elsewhere and are associated with the structural collapse of the habitat (Stuart-Smith et al. 2018). Reduced structural complexity of reefs in North Ari Attoll is also likely to have contributed to long-term declines in fish biomass observed in our surveys.

It was also noted that fish density declined more rapidly than biomass. The high biomass observed in 2016 and the corresponding low density suggests that smaller fish disappeared as soon as 2016 bleaching, strongly impacting density values but not biomass values. The rapid decline in fish density suggests that small-sized fish species disappeared during or just after the bleaching. This phenomenon was recently observed on the Great Barrier reef for smaller planktivorous or coral-dwelling species (Wismer et al. 2019). The coral-related fish group were amongst the most sensitive to the changes in the reef in this study, showing significant declines in biomass each survey year. This further supports the idea that small-sized reef obligates are the most vulnerable to coral habitat disturbance.

Figure 51. Fish on a reef in North Ari Atoll 2019.

Some changes in the biomass between 2015 and 2016 can be attributed to the high variability in both carnivore and planktivore biomass. These groups contribute disproportionately to the biomass as many species in these groups can be large-bodied (carnivores) or present in high numbers (planktivores) or both, e.g. jacks and *Odonus niger*. The three-year gap between 2016 and 2019 surveys prevents a clear understanding of the changes in the fish community over the two years following the bleaching. However, both these groups had declined significantly by 2019 and, with the exception of Rasdhoo (carnivores and planktivores) and Vihamaafaru (planktivores), had less variability in the data. It may be that coral-related planktivores (e.g. damsel fish) became more susceptible to predation during bleaching events (Coker et al. 2009) so these were then rapidly consumed by predators resulting in a decline in prey, leading to further declines in predators, creating a negative feedback. Erosion of structure following coral death would further continue this process (Graham et al. 2007).

The decline in herbivore biomass between 2015 and 2016 appears to have been driven by a significant drop in the biomass of parrotfish that occurred across all management regimes. Herbivore density and biomass are related to structural complexity and the availability of refuge on reefs (Russ 1984, McCook 1997, Verges et al. 2011) and the degradation of reef structure has likely driven the herbivore decline. Another family containing herbivores, surgeonfish, presented non-significant increases in biomass at community and resort reefs between 2015 – 2016, however, this family also contains a number of detritivores species that may have been unaffected by whatever driver impacted the herbivore community, keeping the biomass of surgeonfish higher than that of parrotfish. The overall decline in herbivore biomass, particularly large roving herbivores such as parrotfish, is concerning given the important functional role this group has on reef functioning (Mumby 2006, Nash et al. 2016). Herbivores play a key functional role on reefs by feeding on the algae, preventing them from outcompeting corals, thus favouring coral recruit settling and growth necessary to reef resilience (Cheal et al. 2010). Herbivory is highest on structurally complex reefs (Verges et al. 2011) and the flattening of the reefs will further decrease the effectiveness of herbivores in algae removal.

Corallivores have typically been found to be the most sensitive group to bleaching events as the death of coral results in an immediate loss of food (Pratchett et al. 2006). The 2016 surveys were during the bleaching event, when corals were white but their polyps still alive, therefore would still be alive and able to provide food for corallivorous fish, which explains why their biomass did not drop significantly between 2015 and 2016. The drop occurred between 2016 and 2019, probably soon after the bleached corals died. The family Labridae contains species that have high ecological versatility (Berkström et al. 2012), as such may be more resilient to the impacts of habitat degradation (Munday 2004). However, this did not appear to be the case here as Labrid biomass decreased in a manner similar to the other fish families studied.

This may be an ominous sign for the ecosystem, if these generalist species are struggling to survive there is likely to be severe lack of food and habitat.

There was little variation in the biomass of the fish trophic groups across the management regimes. The biomass between islands was highly variable however, there were many sites which had exceptionally high biomass, particularly within the carnivore and planktivore groups. The presence of medium-bodied schooling planktivores e.g. *Odonus niger, Myripritis adusta* or *Pterocaesio tile* on transects would result in high biomass during the surveys. When grouped by location, biomass of all groups was greater at outer atoll reefs, although the difference was only significant for carnivores, corallivores and coral-related species. This again highlights the impacts of local physical parameters on the reef fish community in North Ari.

The status of the reef fish community in 2019 shows the important role that physical conditions play in determining the condition of reefs in North Ari and their response to the 2016 bleaching event. Though community islands have significantly higher biomass and diversity than resort or uninhabited islands, this difference is driven by the outer atoll reefs of Feridhoo (density and diversity) and Rasdhoo (diversity). Inner atoll islands consistently had lower values for all three fish community metrics, regardless of management regime. When islands were grouped by inner or outer atoll location, outer atoll islands had significantly higher values for fish community density, diversity and biomass.

The complex coral framework provides a range of ecosystem services. Once the coral is dead, its skeleton begins to erode, reducing the structural complexity and hence the range of services it can provide. The widespread reef flattening documented here indicates a worrying trend toward less complex reef habitats that are known to support less abundant (Darling et al. 2017) and diverse (Newman et al. 2015) reef fish assemblages as well as being less resilient to future degradation (Graham et al. 2015). Particularly concerning is the increase in sand as a proportion of the substrate which has reduced the amount of substrate that is suitable for the settlement and growth of benthic organisms such as coral. It may be that, in areas where settlement surface becomes limiting, artificial structures could be used to provide suitable settlement surfaces. This is a method commonly used in the Maldives by many resorts.

4.3. Habitat structure

The habitat structure of most of the reefs in North Ari Atoll became less complex after 2016. The complexity of a reef habitat is largely associated with three-dimensional structure that is created by live corals (Wilson et al. 2007). Coral skeleton is continuously subject to bio-erosion and physical erosion in a reef environment and this is accelerated when corals die. Reefs that experience large scale coral mortality are reported to lose the structural complexity that is maintained by live corals. Therefore, the reduced complexity of reefs at North Ari Atoll, regardless of management regimes, is consistent with observations of degraded reefs losing live coral and the structure created by live corals. Dead and eroded coral skeletons progressively break down into rubble (Glynn and Manzello 2015) are continuously carried away from the reef environment by gravity and water motion (Hughes 1999). Physical and bio-erosion also transforms coral skeletons into calcareous sand (Bianchi et al. 2003). The widespread mortality of corals and associated reduction of reef complexity is repeatedly reported to result in lower fish biomass and abundance of coral associated fish taxa (Graham et al. 2009, Pratchett et al. 2014, 2018), which was also observed in the North Ari islands surveyed here.

4.4. General conclusions

Prior to the bleaching event of 2016, management regime did have an effect on the reef communities, where resorts reefs tended to have healthier ecosystems (Moritz et al. 2017). However, following the 2016 bleaching event, the relationship between management regime and reef condition was weak or non-existent. There was high variability across and within islands surveyed, making absolute comparisons challenging. Each reef area has its own history of ecological and community development, disturbance and recovery that shapes the habitat (Connell et al. 1997, Moritz et al. 2017, Cowburn et al. 2018). It is evident that the individual histories of reefs in North Ari Atoll play a significant role in determining the reef community trajectories. The physical and biological processes on these reefs over long timescales will likely determine the response of the reef community to current and future disturbance events. For example, there was a decline of coral cover on reefs at Alikoirah, Gaathafushi and to a lesser extent Kan'dholhudhoo and Maayafushi associated with COTS outbreaks. It is also important to consider the individual habitat characteristics of reefs such as the island location (outer or inner area of North Ari Atoll), local reef exposure and local reef habitat (terrace, slope or wall) all of which have been associated with taxonomic variation in the composition of coral and reef fish communities (Wilson et al. 2016), and with variation in the abundance of coral recruits (Burt et al. 2010, Price 2010).

Figure 52. Examples of two different reefs showing dominance by complex branching coral growth forms in 2015 (left) and by more simple coral gowth forms in 2019 (right).

Physical features of the reef habitats present at each island are likely to have influenced the extent of observed bleaching. The results reported here suggest that the proportion of corals that bleached was lower on outer island reefs. Reefs exposed to turbulent weather conditions (e.g. waves and wind) are less prone to bleaching, as well as wall or slope reef formations where corals are less exposed to sunlight than upward facing reef terraces. These observations are consistent with reports of reduced bleaching associated with greater cooling or circulation of reef waters and on reefs close to deeper water. Higher wave action or surface unevenness is likely to reduce the irradiance penetrating surface waters in a reef environment, and this is likely to further reduce stress to corals during a bleaching event. Shaded environments may also reduce stress to corals during a bleaching event (Coelho et al. 2017). Island location was a significant determinant of reef community structure. In the survey design three of the four community islands surveyed were outer atoll islands, whereas the opposite was true for resort islands, this resulted in an unbalanced design for the analysis. Future surveys should aim to balance this artefact by adding additional islands. Since the surveys began island use on two islands has changed, the uninhabited island Vihamaafaru is now an industrial chicken farm and Madoogali resort island is not currently operating For the purposes of this study they were still considered as their original management regime.

Here we have attempted to identify how the 2016 bleaching event has impacted the reefs of North Ari Atoll and whether the differences in management regime had altered that response. Though we found some differences between management regimes for some of the fish and benthic groups, it was not possible to draw conclusions about the overall effect of management regime on reef health in 2019. It was observed that physical and biological factors have had the largest influence on current reef condition following the 2016 bleaching event. Studying single events in isolation can provide unclear, or at worst misleading findings and longer term monitoring and deeper analyses are required to understand the processes that dictate the response to any given event and the processes underlying ongoing changes in assemblages (Hughes and Connell 1999). Data from studies such as this should be interpreted carefully as the survey team, environmental conditions and time of day a site was surveyed have all changed over the course of the survey period. The data provides a snapshot of the reef during the survey window. It is not possible to infer the effect these variables may have had on the results.

4.5. Management

Management benefit from resorts has been identified previously (Moritz et al. 2017), yet our findings indicate that any benefit may have been blurred by the impacts of the bleaching event. The reefs on outer atoll islands with access to ocean currents and experience greater water exchange, were in better condition following the bleaching in 2019 than inner atoll reefs which have calmer waters where temperature rises substantially every day, leading to intensified heat stress for corals (Cowburn et al. 2019). Regardless of the management regime in place on an island, it is important that active coral reef management are employed to help protect the reefs. Each management type will have its own challenges. Community islands will need to focus on sustainable community developments, resorts should limit pollution from outflow pipes and sedimentation from beach replenishment and uninhabited islands should not serve as waste disposal sites and have controlled for reef fisheries.

There has been little if any detailed study of the actual difference in impacts between the different management regimes in Maldives, It is presumed here, and elsewhere (Moritz et al. 2017, Cowburn et al. 2018) that due to the different island uses the pressures put on the reef will be considerably different. However, this difference has yet to be quantified to any great degree. It is recommended that studies are undertaken to evaluate these differences, these studies could examine sedimentation rates, fishing pressure, nutrient levels and amount of diving/snorkelling activity. This would allow a better understanding of the cause and effect relationships between management regime and reef condition.

Management recommendations for North Ari Atoll include:

- Sensitive habitats such as sheltered reefs and inner atoll islands have been shown to be more susceptible to the effects of human impacts. Therefore, these areas should be more closely monitored, with tighter restrictions on activities.
- Marine protected areas should be created at the more resilient habitats, such as outer atoll or exposed reef locations. These are more likely to withstand natural disturbances that cannot be managed locally, such as bleaching.

    - This will create “insurance policies” to assist the recovery of other reefs by acting as a source of coral and fish larvae.
- Monitoring international databases e.g. NOAA's coral reef watch, to identify and prepare for bleaching events.
- The limitation of activities likely to cause or accelerate reef erosion or likely to increase the presence of sand and particulate matter in the reef environment. This would be especially important before, during and immediately following bleaching events. Activities include:
    - Sand pumping for beach replenishment
    - Dredging of sand within atolls
    - Land reclamation and island building projects that require depositing sediment near reef areas
    - Dumping of island waste into the sea
- Specifying the protection of herbivorous reef fish species in any management plan. This will help maintain numbers and encourage natural control of the development of turf algae and macroalgae by these fish.
- Monitoring and removal programmes for COTS. They were found to be one of the most significant drivers of coral cover in this study, particularly for *Acropora* corals.
    - COTS surveys can be performed rapidly over large areas using manta tows or snorkel surveys.
    - Where COTS are identified they should be carefully removed from the reef
- Monitoring and enforcement of limits on pollution and nutrient inputs to the marine environment around islands, particularly community and resort islands.

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6. Appendix 1 - Tables

Table A 1. Location of the three sites surveyed at each of the 12 islands.

Island	Site	Latitude Start	Longitude Start	Transect Direction
Bodhufulhudhoo	Bodhufulhudhoo1	4.18760	72.77094	N
Bodhufulhudhoo	Bodhufulhudhoo2	4.18507	72.77098	S
Bodhufulhudhoo	Bodhufulhudhoo3	4.18313	72.77548	NE
Feridhoo	Feridhoo1	4.04846	72.72633	SW
Feridhoo	Feridhoo2	4.05343	72.72795	NW
Feridhoo	Feridhoo3	4.04965	72.73048	SW
Maalhos	Maalhos1	3.98342	72.72141	W
Maalhos	Maalhos2	3.98948	72.71935	W
Maalhos	Maalhos3	3.98274	72.71469	E
Rasdhoo	Rasdhoo1	4.26024	72.99480	SW
Rasdhoo	Rasdhoo2	4.26126	72.98936	SE
Rasdhoo	Rasdhoo3	4.26677	72.98938	SW
Kan'dholhudhoo	Kan'dholhudhoo1	4.00484	72.88089	E
Kan'dholhudhoo	Kan'dholhudhoo2	4.00129	72.88212	W
Kan'dholhudhoo	Kan'dholhudhoo3	4.00304	72.88292	S
Maayafushi	Maayafushi1	4.07110	72.88640	E
Maayafushi	Maayafushi2	4.07668	72.88858	N
Maayafushi	Maayafushi3	4.07302	72.88928	N
Madoogali	Madoogali1	4.09613	72.75587	N
Madoogali	Madoogali2	4.09514	72.75164	NW
Madoogali	Madoogali3	4.09986	72.75226	SE
Velidhoo	Velidhoo1	4.19286	72.81879	E
Velidhoo	Velidhoo2	4.19550	72.82275	SW
Velidhoo	Velidhoo3	4.20119	72.81652	SE
Alikoirah	Alikoirah1	3.94425	72.88158	NW
Alikoirah	Alikoirah2	3.94507	72.87948	NW
Alikoirah	Alikoirah3	3.94266	72.87869	NW
Gaathafushi	Gaathafushi1	4.02842	72.80990	NW
Gaathafushi	Gaathafushi2	4.02204	72.80893	W
Gaathafushi	Gaathafushi3	4.02392	72.81177	S
Madivaru	Madivaru1	4.26724	73.00348	NE
Madivaru	Madivaru2	4.26472	72.99924	N
Madivaru	Madivaru3	4.27185	72.99852	W
Vihamaafaru	Vihamaafaru1	4.11989	72.74473	NW
Vihamaafaru	Vihamaafaru2	4.12615	72.74532	SE
Vihamaafaru	Vihamaafaru3	4.11915	72.74767	W

Table A 2. Width of belt transect used to survey fish family/genus

Family/Genus	Belt width (m)
Acanthuridae	5
Amblyeleotris	2
Balistidae	5
Blenniidae	2
Caesionidae	2
Carangidae	5
Chaetodontidae	5
Apogonidae	2
Chromis	2
Cirrhilabrus	2
Cirrhitidae	2
Corythoichthys	2
Dascyllus	2
Diodontidae	2
Diploprion	2
Ephippidae	5
Fistulariidae	5
Gymnosarda	5
Haemulidae	5
Holocentridae	2
Kyphosidae	5
Labridae	2
Lethrinidae	5
Lutjanidae	5
Microdesmidae	2
Mocanthidae	2
Mullidae	2
Muraenidae	2
Nemateleotris	2
Nemipteridae	2
Ostorhinchus	2
Ostraciidae	5
Oxycheilinus	2
Paracirrhites	2
Parapercis	2
Pempherididae	2
Plesiopidae	2
Pomacanthidae	2
Pomacentridae	2
Priacanthidae	2
Pterois	2
Scaridae	5
Scombridae	5
Scorpaenidae	2
Serranidae	5
Siganidae	5
Synodontidae	2
Tetraodontidae	2
Tripterygiidae	2
Zanclidae	5

Table A 3. Median percent cover and interquartile range (IQR) of *Acropora* size classes observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

	Community						Resort						Uninhabited					
	2015		2016		2019		2015		2016		2019		2015		2016		2019	
Size (cm)	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
0-5	4.0	2.0, 6.0	0.4	0.2, 1.6	0.8	0.4, 2.0	6.0	4.0, 11.6	1.2	0.4, 2.1	0.8	0.8, 2.0	4.8	4.2, 7.2	0.8	0.4, 2.0	0.8	0.4, 1.4
6-10	0.3	0.1, 0.8	0.1	0.0, 0.3	0.1	0.0, 0.2	0.7	0.3, 1.4	0.3	0.1, 0.5	0.0	0.0, 0.1	0.4	0.3, 0.7	0.0	0.0, 0.2	0.1	0.0, 0.1
11-20	0.8	0.1, 1.5	0.1	0.0, 0.4	0.4	0.1, 0.7	1.1	0.5, 2.6	0.4	0.1, 0.7	0.0	0,0 0.1	1.0	0.4, 1.6	0.1	0.0, 0.4	0.0	0.0, 0.2
21-40	0.3	0.0, 0.8	0.1	0.0, 0.4	0.3	0.0, 0.9	0.8	0.3, 1.4	0.2	0.1, 0.6	0.0	0.0, 0.0	0.8	0.2, 1.2	0.1	0.0, 0.4	0.0	0.0, 0.0
41-65	0.0	0.0, 0.1	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.2	0.0	0.0, 0.1	0.0	0.0 0.0	0.1	0.0, 0.2	0.0	0.0, 0.0	0.0	0.0, 0.0
>66	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.2	0.0	0.0, 0.1	0.0	0.0, 0.0	0.1	0.0, 0.3	0.0	0.0, 0.0	0.0	0.0, 0.0

Table A 4..Median percent cover and interquartile range (IQR) of *Porites* size classes observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

	Community						Resort						Uninhabited					
	2015		2016		2019		2015		2016		2019		2015		2016		2019	
Size (cm)	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
0-5	2.0	1.2, 2.8	0.4	0.4, 0.8	0.8	0.4, 1.4	2.8	0.8, 4.2	0.4	0.2, 0.7	0.8	0.4, 1.2	2.6	1.6, 4.3	0.5	0.4, 0.8	1.0	0.4, 1.7
6-10	0.3	0.2, 0.5	0.1	0.0, 0.4	0.1	0.0, 0.2	0.2	0.1, 0.4	0.1	0.0, 0.3	0.1	0.0, 0.4	0.4	0.1, 0.7	0.1	0.0, 0.3	0.1	0.1, 0.3
11-20	0.6	0.4, 0.8	0.2	0.0, 0.4	0.6	0.3, 1.1	0.3	0.2, 0.6	0.1	0.0, 0.3	0.2	0.0, 0.6	0.6	0.2, 1.3	0.1	0.0 0.5	0.2	0.0, 0.7
21-40	0.2	0.1, 0.4	0.1	0.0, 0.2	0.3	0.1, 0.7	0.1	0.1, 0.3	0.0	0.0, 0.1	0.0	0.0, 0.2	0.4	0.1, 0.5	0.0	0.0, 0.3	0.0	0.0, 0.5
41-65	0.0	0.0, 0.1	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.1	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.1	0.0	0.0, 0.0	0.0	0.0, 0.0
>66	0.0	0, 0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0 0.0	0.0	0.0, 0.0

Table A 5. Median percent cover and interquartile range (IQR) of *Pocillopora* size classes observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019

	Community						Resort						Uninhabited					
	2015		2016		2019		2015		2016		2019		2015		2016		2019	
Size (cm)	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
0-5	3.2	2.4, 5.0	0.4	0.2, 1.2	1.4	0.4, 2.8	2.0	1.1, 3.6	0.4	0.2, 0.8	1.2	0.4, 2.0	2.0	0.8, 4.0	0.4	0.4, 1.1	1.2	0.8, 2.0
6-10	0.1	0.0, 0.2	0.0	0.0, 0.1	0.0	0.0, 0.1	0.0	0.0, 0.1	0.0	0.0, 0.1	0.0	0.0, 0.1	0.1	0.0, 0.2	0.0	0.0, 0.1	0.1	0.0, 0.1
11-20	0.1	0.1, 0.2	0.0	0.0, 0.1	0.1	0.0, 0.5	0.2	0.1, 0.2	0.0	0.0, 0.1	0.0	0.0, 0.1	0.1	0.0, 0.3	0.0	0.0, 0.1	0.0	0.0, 0.2
21-40	0.1	0.0, 0.1	0.0	0.0, 0.1	0.1	0.0, 0.3	0.1	0.0, 0.2	0.0	0.0, 0.1	0.0	0.0, 0.1	0.2	0.1, 0.3	0.0	0.0, 0.1	0.0	0.0, 0.1
41-65	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0
>66	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0.0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0

Table A 6. Median percent cover and interquartile range (IQR) of *Pavona* size classes observed on point intercept transects in North Ari Atoll surveys undertaken in 2015, 2016 and 2019.

	Community						Resort						Uninhabited					
	2015		2016		2019		2015		2016		2019		2015		2016		2019	
Size (cm)	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR	Median	IQR
0-5	3.2	1.6, 4.8	1.1	0.4, 3.2	5.2	4.0, 7.4	4.0	1.6, 6.8	0.6	0.4, 2.8	6.2	3.3, 8.4	8.0	4.2, 12.2	0.8	0.4, 2.2	5.2	2.9, 8.3
6-10	0.5	0.3, 0.8	0.2	0.0, 0.5	0.1	0.0, 0.3	0.2	0.1, 0.5	0.1	0.0, 0.4	0.1	0.0, 0.2	0.3	0.1, 0.7	0.0	0.0, 0.3	0.1	0.0, 0.3
11-20	0.0	0.0, 0.1	0.0	0.0, 0.1	0.3	0.1, 0.6	0.1	0.0, 0.3	0.0	0.0, 0.2	0.1	0.0, 0.5	0.2	0.1, 0.5	0.0	0.0 0.1	0.1	0.0, 0.4
21-40	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.2	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.2	0.0	0.0, 0.0	0.0	0.0, 0.1
41-65	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0

>66	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0	0.0	0.0, 0.0

Table A 7. Total number of coral colonies bleached and proportion of total coral colonies dead by genera. Data from all surveys on 2016 survey of North Ari Atoll

Genus	Number of colonies bleached	Proportion dead	
		Mean	S.E.
Acropora	3188	26.3	2.5
Porites	1972	4.3	1.13
Pavona	1224	1.1	4.4
Pocillopora	624	0.0	0.0
Leptoseris	516	0.6	0.39
Goniastrea	391	10.7	2.64
Montipora	349	1.1	0.47
Fungia	266	18.1	2.93
Psammocora	257	1.2	1.07
Favites	216	1.8	1.27
Leptastrea	195	2.3	1.32
Goniopora	173	0.4	0.27
Galaxea	155	6.2	1.96
Platygyra	120	3.5	1.79
Astreopora	109	0.0	0.0
Cyphastrea	87	0.5	0.35
Echinopora	64	5.5	1.97
Montastraea	60	5.2	1.86
Coscinaraea	56	0.0	0.0
Favia	49	1.5	0.83
Gardineroseris	45	0.0	0.0
Pachyseris	38	5.8	2.08
Symphyllia	36	0.0	0.0
Alveopora	32	0.0	0.0
Merulina	26	0.0	0.0
Caulastrea	25	33.3	4.33
Echinophyllia	24	5.9	2.33
Lobophyllia	24	0.0	0.0
Pectinia	21	7.1	2.57
Turbinaria	20	3	0.97
Plesiastrea	19	0.0	0.0
Diploastrea	18	14.3	3.49
Hydnophora	17	0.0	0.0
Physogyra	9	0.0	0.0
Acanthastrea	8	0.0	0.0
Halomitra	8	37.5	4.98
Ctenactis	7	0.0	0.0
Mycedium	6	0.0	0.0
Podabacia	6	0.0	0.0
Oxypora	5	20	4.3
Cycloseris	2	0.0	0.0
Oulophyllia	2	0.0	0.0
Leptoria	1	0.0	0.0
Unknown	1	0.0	0.0

Table A 8. Table of fish genera observed the on belt transect surveys

Family	Genus	2015	2016	2019
Acanthuridae	*Acanthurus*	X	X	X
Acanthuridae	*Ctenochaetus*	X	X	X
Acanthuridae	*Naso*	X	X	X
Acanthuridae	*Zebrasoma*	X	X	X
Apogonidae	*Cheilodipterus*	X	X	X
Apogonidae	*Ostorhinchus*	X	X	X
Apogonidae	*Pristiapogon*		X	
Aulostomidae	*Aulostomus*	X	X	
Balistidae	*Balistapus*	X	X	X
Balistidae	*Balistoides*	X	X	X
Balistidae	*Melichthys*	X	X	X
Balistidae	*Odonus*	X	X	X
Balistidae	*Pseudobalistes*		X	
Balistidae	*Rhinecanthus*		X	
Balistidae	*Sufflamen*	X	X	X
Blennidae	*Meiacanthus*	X	X	X
Blenniidae	*Blenniidae*	X		X
Blenniidae	*Ecsenius*	X		X
Blenniidae	*Plagiotremus*	X	X	X
Caesionidae	*Caesio*	X	X	X
Caesionidae	*Pterocaesio*	X	X	X
Carangidae	*Carangoides*	X		
Carangidae	*Caranx*	X	X	X
Carangidae	*Elagatis*			X
Carangidae	*Gnathanodon*		X	
Carangidae	*Trachinotus*		X	
Carcharhinidae	*Triaenodon*	X	X	
Chaetodontidae	*Chaetodon*	X	X	X
Chaetodontidae	*Forcipiger*	X	X	X
Chaetodontidae	*Hemitaurichthys*	X	X	X
Chaetodontidae	*Heniochus*	X	X	X
Cirrhitidae	*Cirrhitichthys*	X		X
Cirrhitidae	*Paracirrhites*	X	X	X
Congridae	*Gorgasia*	X		
Diodontidae	*Diodon*		X	X
Echeneidae	*Echeneis*		X	
Ephippidae	*Platax*	X	X	X
Fistulariidae	*Fistularia*	X	X	X
Gobiidae	*Amblyeleotris*	X		X
Gobiidae	*Amblygobius*	X		X
Gobiidae	*Gobiodon*	X		
Gobiidae	*Koumansetta*	X	X	X
Haemulidae	*Plectorhinchus*	X	X	X
Holocentridae	*Myripristis*	X	X	X
Holocentridae	*Neoniphon*	X	X	X
Holocentridae	*Sargocentron*	X	X	X
Kyphosidae	*Kyphosus*	X	X	X
Labridae	*Ampses*	X	X	X
Labridae	*Bodianus*	X	X	X
Labridae	*Cheilinus*	X	X	X
Labridae	*Cirrhilabrus*	X	X	X
Labridae	*Coris*	X	X	X

Family	Genus	2015	2016	2019
Labridae	*Epibulus*	X	X	X
Labridae	*Gomphosus*	X	X	X
Labridae	*Halichoeres*	X	X	X
Labridae	*Hemigymnus*	X	X	X
Labridae	*Labrichthys*	X	X	X
Labridae	*Labroides*	X	X	X
Labridae	*Macropharyngodon*	X	X	X
Labridae	*Novaculichthys*	X		
Labridae	*Oxycheilinus*	X	X	X
Labridae	*Pseudocheilinus*	X	X	X
Labridae	*Pseudocoris*	X		
Labridae	*Pseudodax*	X	X	X
Labridae	*Stethojulis*	X	X	X
Labridae	*Thalassoma*	X	X	X
Labridae	*Wetmorella*	X		
Lethrinidae	*Gthodentex*	X	X	X
Lethrinidae	*Lethrinus*	X	X	X
Lethrinidae	*Monotaxis*	X	X	X
Lutjanidae	*Aphareus*	X	X	X
Lutjanidae	*Aprion*	X	X	X
Lutjanidae	*Lutjanus*	X	X	X
Lutjanidae	*Macolor*	X	X	X
Microdesmidae	*Nemateleotris*	X	X	X
Microdesmidae	*Ptereleotris*	X	X	X
Mocanthidae	*Cantherhines*	X	X	
Mocanthidae	*Oxymocanthus*	X	X	
Mocanthidae	*Paraluteres*	X	X	X
Monacanthidae	*Amanses*	X	X	
Monacanthidae	*Pervagor*	X	X	X
Mullidae	*Mulloidichthys*	X		
Mullidae	*Parupeneus*	X	X	X
Muraenidae	*Echid*			X
Muraenidae	*Gymnothorax*	X	X	X
Myliobatidae	*Aetobatus*	X	X	
Nemipteridae	*Scolopsis*	X	X	X
Ostraciidae	*Ostracion*	X	X	X
Pempherididae	*Parapriacanthus*	X	X	X
Pempherididae	*Pempheris*	X	X	X
Pinguipedidae	*Parapercis*	X	X	X
Plesiopidae	*Calloplesiops*		X	X
Pomacanthidae	*Apolemichthys*	X	X	X
Pomacanthidae	*Centropyge*	X	X	X
Pomacanthidae	*Pomacanthus*	X	X	
Pomacanthidae	*Pygoplites*	X	X	X
Pomacentridae	*Abudefduf*	X	X	
Pomacentridae	*Amblyglyphidodon*	X	X	X
Pomacentridae	*Amphiprion*	X	X	X
Pomacentridae	*Chromis*	X	X	X
Pomacentridae	*Dascyllus*	X	X	X
Pomacentridae	*Plectroglyphidodon*	X	X	X
Pomacentridae	*Pomacentrus*	X	X	X
Priacanthidae	*Priacanthus*	X	X	X
Ptereleotris	*Ptereleotris*			X
Scaridae	*Calotomus*	X	X	X
Scaridae	*Cetoscarus*	X	X	X
Scaridae	*Chlorurus*	X	X	X
Scaridae	*Hipposcarus*	X	X	X
Scaridae	*Scarus*	X	X	X
Scombridae	*Euthynnus*	X	X	X

Family	Genus	2015	2016	2019
Scombridae	*Gymnosarda*	X	X	X
Scorpaenidae	*Pterois*	X	X	X
Scorpaenidae	*Scorpaenopsis*			X
Serranidae	*Aethaloperca*	X	X	X
Serranidae	*Anyperodon*	X	X	X
Serranidae	*Cephalopholis*	X	X	X
Serranidae	*Diploprion*	X		X
Serranidae	*Epinephelus*	X	X	X
Serranidae	*Gracila*	X	X	X
Serranidae	*Nemanthias*	X	X	X
Serranidae	*Plectropomus*	X		X
Serranidae	*Pseudanthias*	X	X	X
Serranidae	*Variola*	X	X	X
Siganidae	*Siganus*	X	X	X
Sygnathidae	*Corythoichthys*			X
Synodontidae	*Saurida*		X	
Synodontidae	*Synodus*	X	X	X
Tetraodontidae	*Arothron*	X	X	X
Tetraodontidae	*Canthigaster*	X	X	X
Tripterygiidae	*Helcogramma*	X	X	X
Zanclidae	*Zanclus*	X	X	X

7. Appendix 2 – Figures

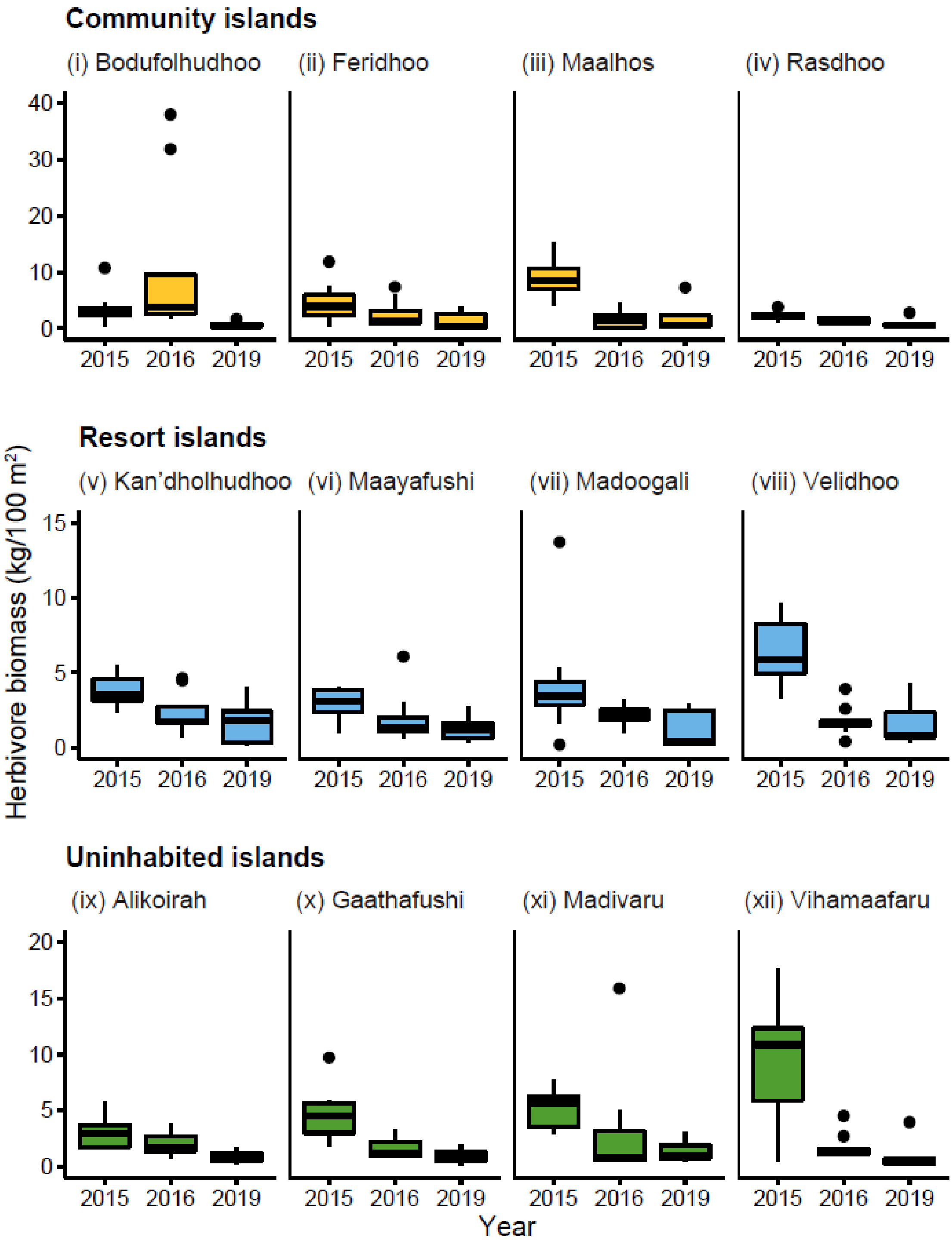

Figure A2 1. Herbivore fish biomass boxplots for the 12 islands surveyed in 2015, 2016 and 2019.

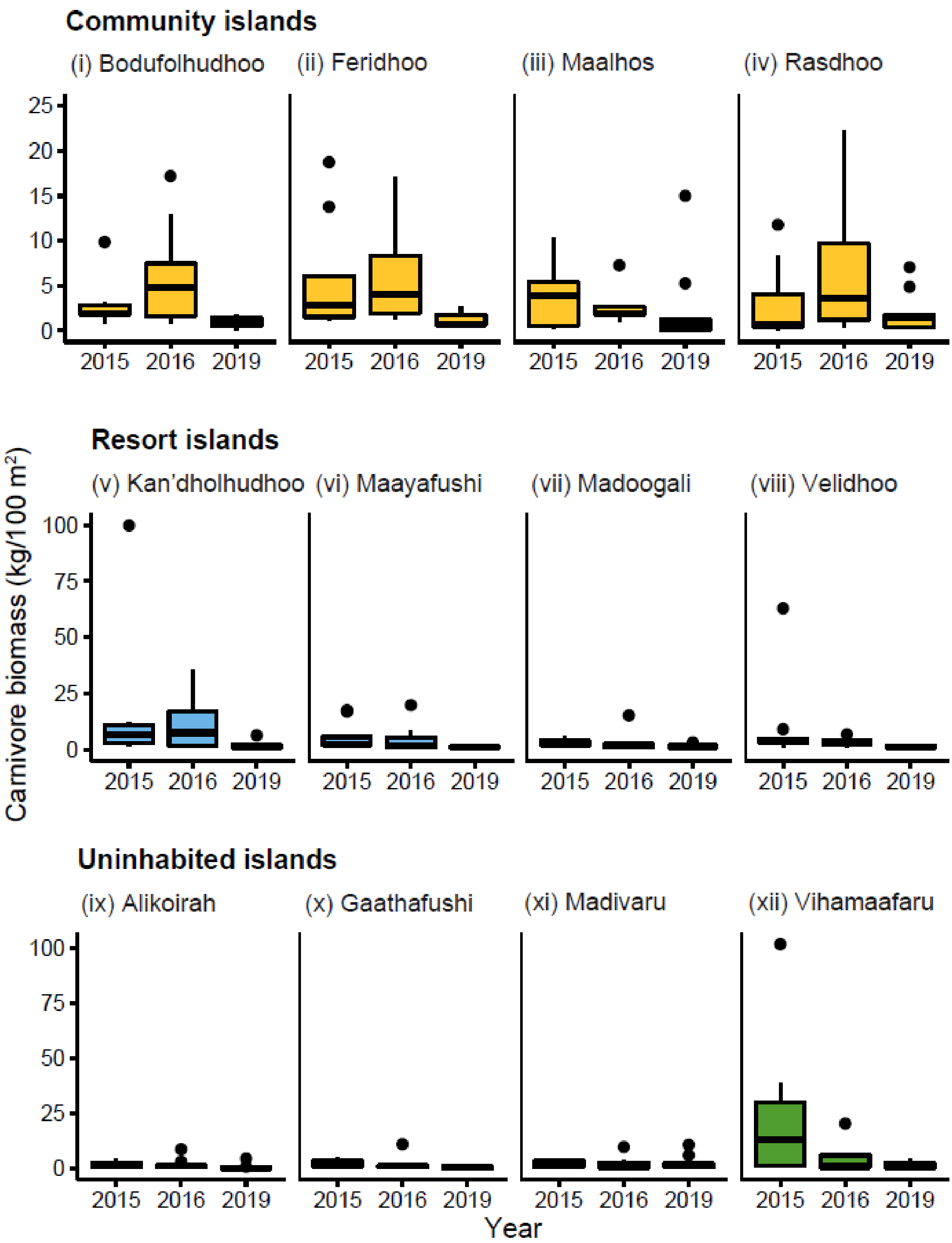

Figure A2 2. Carnivore fish biomass boxplots for the 12 islands surveyed in 2015, 2016 and 2019.

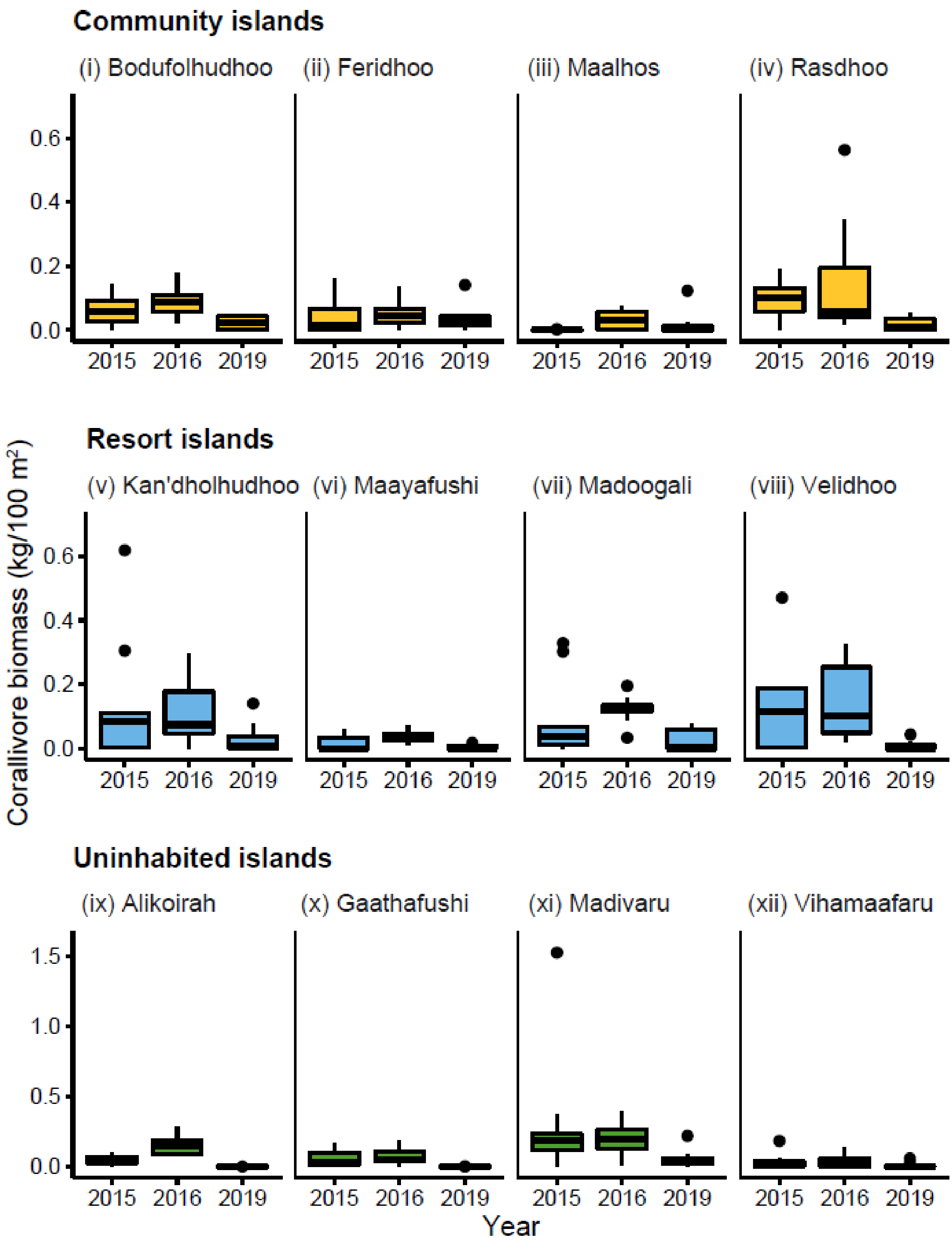

Figure A2 3. Corallivore fish biomass boxplots for the 12 islands surveyed in 2015, 2016 and 2019.

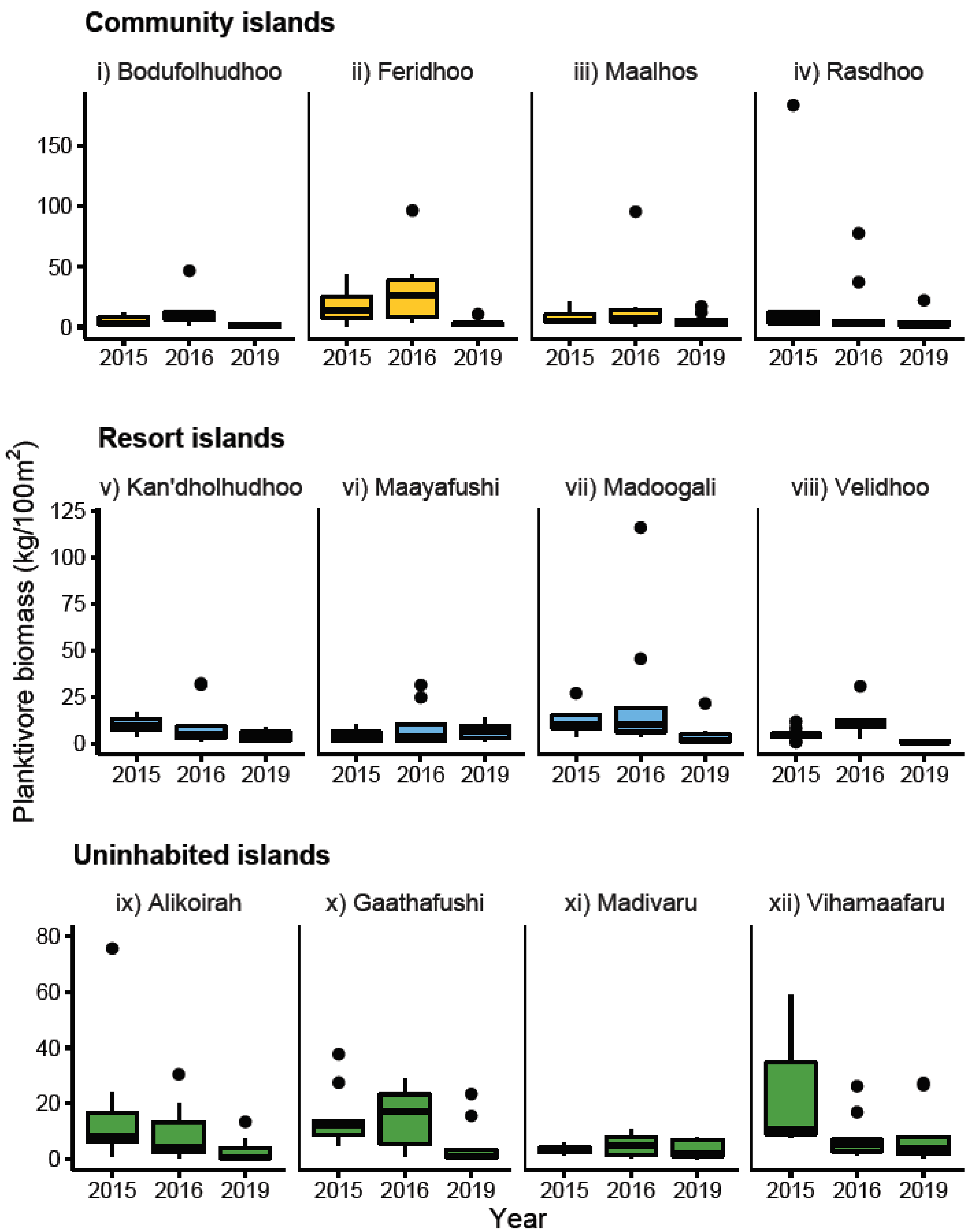

Figure A2 4. Planktivore fish biomass boxplots for the 12 islands surveyed in 2015, 2016 and 2019.

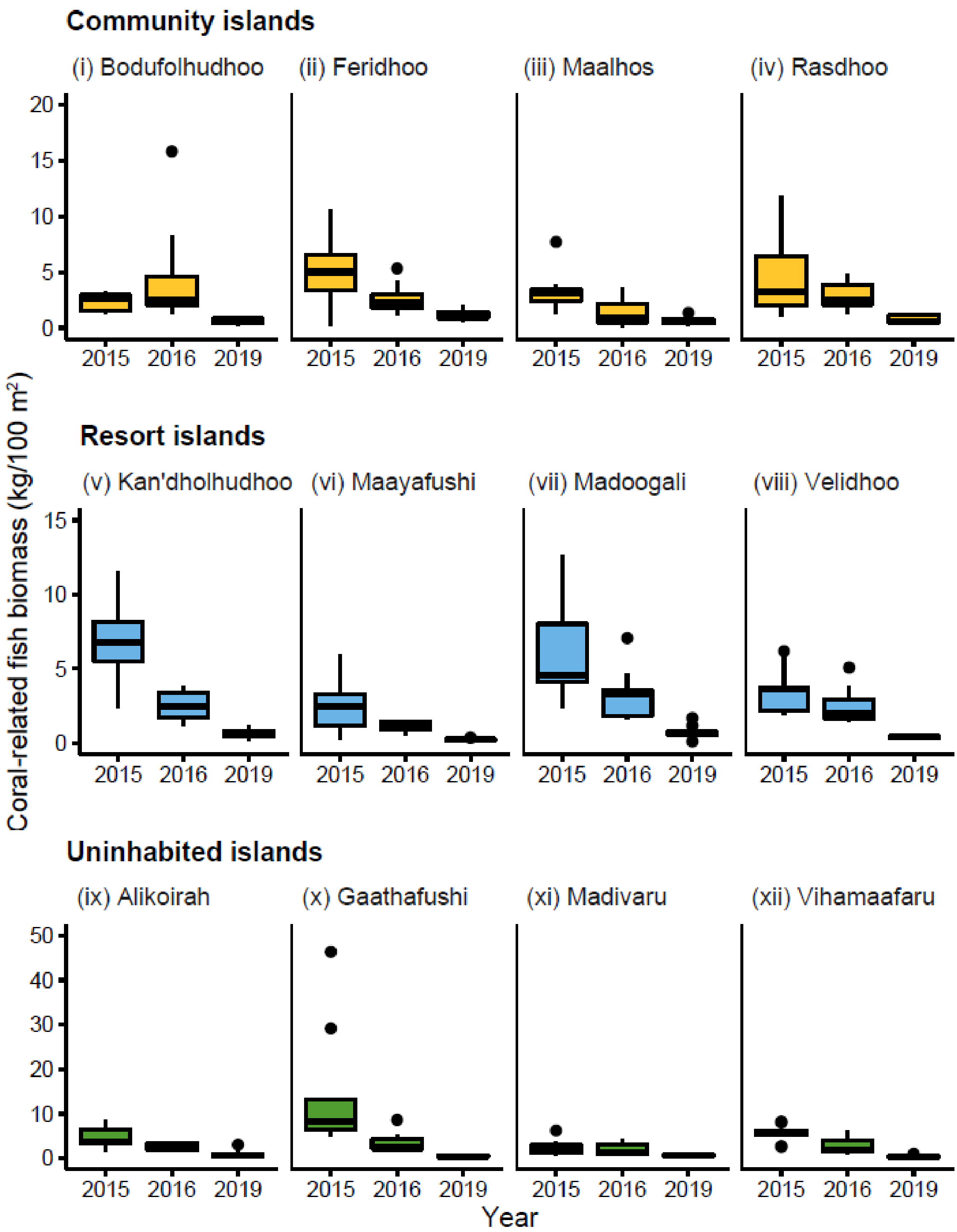

Figure A2 5. Coral-related fish biomass boxplots for the 12 islands surveyed in 2015, 2016 and 2019.

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